CONTRIBUTIONS
TO ENTOMOLOGY

**72** (1): 037–066
2022

© 2022 Senckenberg Gesellschaft für Naturforschung

SENCKENBERG

# Contributions to a revision of the *Hylaeus brevicornis* group (Hymenoptera, Anthophila, Colletidae)

With 62 figures

HOLGER H. DATHE [1]

[1] Senckenberg Deutsches Entomologisches Institut, Eberswalder Straße 90, 15374 Müncheberg, Germany. – holger.dathe@senckenberg.de

Published on 2022-07-31
DOI: 10.3897/contrib.entomol.72.e87230

## Abstract

The *Hylaeus brevicornis* group of the subgenus *Dentigera* is defined and revised. A total of 22 species are included in the group, their circumscription and identification using morphological characters is described and discussed, and their distribution is studied. Three species from Lebanon and Nepal are described as new to science. The hitherto unknown females of *Hylaeus* (*Dentigera*) *alievi* DATHE & PROSHCHALYKIN, 2021 and *Hylaeus* (*Dentigera*) *biarmicus* (WARNCKE, 1992) are described for the first time. An integrative revision of the group involving gene sequencing is being prepared.

## Nomenclatural acts

*Hylaeus* (*Dentigera*) *gutichauris* spec. nov. – urn:lsid:zoobank.org:act:47161A86-73EF-45C0-B059-E9910630CF6C
*Hylaeus* (*Dentigera*) *kaigaonis* spec. nov. – urn:lsid:zoobank.org:act:9EFEF7EA-3BFE-4940-85D2-AA45D942DD00
*Hylaeus* (*Dentigera*) *mirae* spec. nov. – urn:lsid:zoobank.org:act:4ACDE979-96A2-4D60-B500-B11FA26F9FA1
*Prosopis sinaitica* ALFKEN, 1938 = *Hylaeus pallidicornis* MORAWITZ, 1876 – syn. nov.

## Key words

taxonomy, nomenclature, new species, synonyms, distribution data, male terminalia

## Zusammenfassung

Die *Hylaeus-brevicornis*-Gruppe der Untergattung *Dentigera* wird definiert und revidiert. Insgesamt sind 22 Arten in die Gruppe aufgenommen, sie werden anhand morphologischer Merkmale untersucht und definiert; dazu wird ihre Verbreitung angegeben. Aus dem Libanon und Nepal werden drei Arten als neu für die Wissenschaft beschrieben. Die bisher unbekannten Weibchen von *Hylaeus* (*Dentigera*) *alievi* DATHE & PROSHCHALYKIN, 2021 und *Hylaeus* (*Dentigera*) *biarmicus* (WARNCKE, 1992) werden erstmals vorgestellt. Damit wird die Gruppe auch für eine integrative Revision mit genetischer Sequenzierung vorbereitet.

## Introduction

A revision of the species of the *Hylaeus brevicornis* group has been repeatedly demanded, but never realised. This was mainly due to an insufficient data base, in terms both of sample availability and geographic coverage. In recent years, more and more papers have been published in which several "white spots" on the map have been erased by new faunistic and taxonomic findings, so that in the meantime a more informed assessment of their biodiversity is possible. The most easterly occurrences of *Dentigera* are from central China (*Hylaeus luna* Chen & Xu, 2009) and eastern Mongolia. The joint work of Proshchalykin and Dathe (Proshchalykin & Dathe 2016, 2017, 2018, 2021; Dathe & Proshchalykin 2016, 2017, 2018) led to significant progress in the systematic recording of fauna from the Far East of Russia through Mongolia and northern China to the Caucasus. Dathe was able to gain substantial experience over larger parts of the northern Palaearctic, especially from Asia Minor, the Middle East and Central Asia, through further productive collaboration with partners in Israel (Mandelik and collaborators since 2007), Turkey (Özbek & Dathe 2020), Lebanon (Boustani et al. 2021), Morocco (Lhomme et al. 2021) and the Aegean Islands (Petanidou and collaborators since 2015). Furthermore, in the Himalayas a new species of the brevicornis group was discovered by Ikudome & Dathe (2021, *Hylaeus kumari*), as well as – described here – *Hylaeus gutichauris* spec. nov. and *Hylaeus kaigaonis* spec. nov.

## Material and methods

The studies are based on my determinations of about 7,500 specimens studied during four decades. Species of the *Hylaeus brevicornis* group are mainly western Palaearctic, with a certain concentration around the eastern Mediterranean region (Greece, Lebanon, Israel, Cyprus), but in recent years more extensive collections from the Caucasus, Turkey and Central Asia have also been evaluated. The specimens were conventionally needle-pinned, and the terminalia of interesting and doubtful males were prepared and partly photographed. The majority of the specimens was returned to the senders and they are now in their collections; mostly only duplicates were retained in the SDEI collection as voucher specimens.

With the exception of *Hylaeus* (*Dentigera*) *luna* Chen & Xu, 2009, all types were examined and in males genitalized. The types of Förster (coll. ZSS Munich), Morawitz (ZISP St. Petersburg), Nylander (NHRM Stockholm), Alfken (ZMB Berlin), Nurse (NHML London) and Warncke (OLM Linz) were borrowed. Of particular value was the loan of specimens from the Natural History Museum Vienna, which have only recently been COI barcoded (Schoder 2018). Five species, *Hylaeus brevicornis* Nylander, *H. gredleri* Förster, *H. imparilis* Förster, *H. intermedius* Förster as well as (presumably) *H. kahri* Förster had been collected syntopically and comparatively studied. Thus, it was possible to apply baseline standards of morphological comparison in this study, correlated with these genetic data. Simultaneously, this also created a connection to the BOLD database (Ratnasingham & Hebert 2007). Major changes in our view of the mentioned taxa did not arise, even after the type comparisons.

In an early paper (Dathe 1980: 213) I had recommended that the terminalia should be routinely extracted from the anal aperture. This was not good advice, because proper dissection requires some experience and particular care. The sternites are so firmly attached to the tagmata that the metasoma is often stretched excessively when they are pulled out. The individual parts have to be cut off at specific sites. This is best done under the protection of water or gel, otherwise the elastic particles can spring away and are easily lost. The genital capsule is somewhat more robust, but the sternites are very sensitive.
It is not recommended to try maceration with potassium hydroxide. Although this removes disturbing connective tissue and separates the parts well, they also deform considerably. In the process, they are discolored so that they can hardly be found again in the gel. They dry out ex situ anyway and can lose their functional structure as a result. Especially the extremely delicate bristles on the apical lobes are easily lost. In any case, being very small, they are at the limit of optical resolution, so that they are often barely perceptible even with a good microscope. This study therefore prefers to use drawings for the depiction of sterna 7 and 8, which also include an interpretation.

The morphological terminology of Michener (2007) is basically followed. Some terms that find special use in the genus *Hylaeus* are explained in detail in Özbek & Dathe (2020: 275 ff.). The following abbreviations are used in the description of the new species: N – Number of specimens examined; TL – total length; WL – wing length; HL:HW – head length to width ratio; UHW:LHW – upper face width to lower face width ratio; ScL:ScW – scape length to width ratio; CL:CW – clypeus length to width ratio; with indication of the range, in brackets the mean value. The tagmata of the metasoma, terga (T) and sterna (S), are named by their initial letters and the number of their sequence; T1 and S1, respectively, are the visible basal elements, which in comparative anatomical terms are known to correspond to tergite 2 and sternite 2. GC refers to the genital capsule.
The specimens were studied with a stereomicroscope Olympus SZX12, the photos taken with a Leica camera and Leica Application Suite vs. 4.12. The stacks of digital images were processed using Helicon Focus 7.7.4.

In describing the geographic distribution of species, the following terms are used: *Asia minor* – Turkey (Asian part); *Near East* – Arab states (Syria, Lebanon, Jordan, Iraq), Iran and Israel; *Middle East* – Afghanistan, Pakistan; *Central Asia* – Kazakhstan, Uzbekistan, Turkmenistan, Kyrgyzstan, Tajikistan; *Far East* – Russian Far East. Mongolia, China and Japan are indicated separately.

The collections mentioned in the text are abbreviated as follows:

| | |
|---|---|
| ELKU Fukuoka | Entomological Laboratory, Faculty of Agriculture, Kyushu Univ., Fukuoka, Japan |
| ETH Zurich | Entomologische Sammlung, Eidgenössische Technische Hochschule Zürich, Switzerland |
| FSCV Vladivostok | Federal Scientific Center of the East Asia Terrestrial Biodiversity, Russian Academy of Sciences, Far Eastern Branch, Vladivostok, Russia |
| MCAU Beijing | Entomological Museum, China Agricultural University, Beijing, China |
| MBOU | collection Mira Boustani, Université de Mons, Belgium |
| MNHN Paris | Muséum national d'Histoire naturelle, Paris, France |
| NHML London | Natural History Museum, London, Great Britain |
| NHMW Vienna | Naturhistorisches Museum Wien, Austria |
| NHRM Stockholm | Naturhistoriska Riksmuseet, Stockholm, Sweden |
| OLM Linz | Biologiezentrum Linz, Oberösterreichisches Landesmuseum, Linz-Dornach, Austria |
| SDEI Müncheberg | Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany |
| ZISP St. Petersburg | Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia |
| ZMB Berlin | Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany |
| ZMMU Moscow | Zoological Museum, Lomonosov Moscow State University, Moscow, Russia |
| ZSS Munich | Zoologische Staatssammlung, München, Germany |

## Characterisation of the *Hylaeus brevicornis* group

The species of *Hylaeus* subgenus *Dentigera* occur throughout Europe up to 64°N latitude and reach the Himalayan massif, Central Asia and central China in the east, via the Near East, Iran and Afghanistan. The vast majority of the known species can be easily assigned morphologically to two groups, which are primarily distinguished by the structure of their penis valves. The *Hylaeus conformis* group with eight species (in Michener 2000: 195 "*brachycephalus* group") has been studied in detail by Dathe (2006). In these animals, the penis valves appear in dorsal view as elongated with more or less curved keels with broad inward surfaces, which almost conceal the inner tooth which gives them their name (Dathe 2006: 76).

The other large group, which we have named the *Hylaeus brevicornis* group, shows narrow curved valvae in dorsal view, which have a pointed inner tooth basally and remain separated distally, like an open horseshoe. These 22 species form the large majority in the subgenus. A recent study on the fauna of the Caucasus (Proshchalykin & Dathe 2021) even revealed a certain dominance of the group in the eastern high mountains. A separate development can be seen in the Himalayas. In the Mediterranean region, too, certain species are frequent and represented by larger numbers of individuals.

The species exhibit a number of other very similar characters in both sexes, and neither is it easy to interpret levels of variability, so that the taxonomic study of the *brevicornis* group as a whole must be regarded as unfinished. A way out of this situation can only be provided by an integrative combination with molecular genetic studies, as already demonstrated by the resilient results of the first such studies (Schmidt et al. 2015, Schoder 2018). It would be futile here to present another classical morphological paper, if the best modern methods did not also require appropriate concepts. On the basis of data collection over several decades, obtained from thousands of animals studied, my experiences will be compiled here. A special role is played by the comparative study of such genital structures as have not so far been considered.

Some species in the subgenus cannot be assigned to either group: *Hylaeus rubicola* Saunders, 1850 (close to *conformis*) as well as *H. biarmicus* (Warncke, 1992) and *H. chukar* (Warncke, 1992) (close to *brevicornis*).

The species of the *Hylaeus brevicornis* group are at most medium-sized, but usually small to very small, and hardly hairy. They are difficult to distinguish: often this is only possible with some certainty using complexes of characters. The males have differently expanded scapes, from slender to almost spherical in frontal view; the sternum 3 bears paired callosities, occasionally also a single strong process. The male terminalia are of special importance. All the species have a compact, round head with normal genae and a shallowly convex face, the clypeus is rarely

depressed (*Hylaeus glacialis* Morawitz), the malae are narrow. The entire integument of the mesosoma and metasoma is transversely shagreen and always distinctly punctate, although the punctation is variable in strength and density. Males and females of the same species often differ in the size and density of the punctation and in the shininess of the basal metasomal tergites. A first glance at tergum 1 and the mesopleura usually leads in the right direction, but subsequently the determination becomes subtle. A useful character of females of the group is the tridentate mandibles; there are also such in species of other subgenera, for example in *Lambdopsis*, but together with the sculptural characters and the observation that the foveae faciales do not extend to the vertex (as in *Paraprosopis* species), the initial assignment is quite straightforward.

As a result, the following *Hylaeus* species of the *brevicornis* group were ascertained in the area:

| | | | |
|---|---|---|---|
| 1 | *acer* Dathe, 1980 | 13 | *mirae* spec. nov. |
| 2 | *alievi* Dathe & Proshchalykin, 2021 | 14 | *pallidicornis* Morawitz, 1876 |
| 3 | *breviceps* Morawitz, 1876 | 15 | *petzi* Dathe & Proshchalykin, 2018 |
| 4 | *brevicornis* Nylander, 1852 | 16 | *punctus* Förster, 1871 |
| 5 | *giresunus* (Warncke, 1992) | 17 | *syriacus* (Alfken, 1936) |
| 6 | *glacialis* Morawitz, 1872 | | |
| 7 | *gredleri* Förster, 1871 | | **Species of the Himalayas** |
| 8 | *imparilis* Förster, 1871 | 18 | *kashmirensis* (Nurse, 1903) |
| 9 | *intermedius* Förster, 1871 | 19 | *vetustus* (Nurse, 1903) |
| 10 | *kahri* Förster, 1871 | 20 | *kumari* Dathe & Ikudome, 2021 |
| 11 | *laticeps* Morawitz, 1876 | 21 | *gutichauris* spec. nov. |
| 12 | *luna* Chen & Xu, 2009 | 22 | *kaigaonis* spec. nov. |

*Hylaeus* (*Dentigera*) *biarmicus* (Warncke, 1992) and *Hylaeus* (*Dentigera*) *chukar* (Warncke, 1992) are added below to complete the subgenus *Dentigera*, together with my revision of the *conformis* group (Dathe 2006).

## The genital armature of the males

The terminalia or genital armature of males are generally composed of three parts, the genital capsule and sterna 7 and 8 (Figs 1, 2). The genital capsule of bees is a relatively large, well-chitinised pincer-like formation, retracted into the end of the body below the last visible tergites. It is stretched out for mating. Sometimes the genital capsule is called the actual copulatory apparatus, but this is not quite correct, because presumably the other two sternites, which lie in situ under the capsule (Fig. 1), also have a special function in mating, which is however not known. An argument for this assumption is the fact that this "triad" is present in all bee taxa. During dissection, another very delicate structure (Fig. 1: T8), which can be attributed to the terga, is regularly found on the underside of the last visible tergite, adjacent to the genital capsule.

**Fig. 1**: *Hylaeus kahri* ♂, Terminalia in situ, ventral view. GC – genital capsule. S7, S8 – sterna 7 and 8. T6–T8 – terga 6 to 8.

Excellent illustrations of genital capsules of bees, especially bumblebees, were given by Bertsch (2019) as electron microscopic 3D raster photos. In *Hylaeus* species, the genital capsule is comparatively reduced. Here, it consists of a basal ring (gonobase) into which two movable gonoforcipes are inserted. Sometimes gonocoxite and gonostylus can be distinguished from the gonoforceps. The usual dorsal view shows a pair of penis valves between the gonoforcipes. The actual penis has a membranous structure and is not readily visible on specimens. Other structures like the paired volsellae and spatha inside the capsule are also barely visible; they are therefore of no importance for our present study. According to the illustrations in Méhelÿ (1935), who used transmitted light preparations as templates, one can also assume specific formation.

The last sternites of the males, called sternum 7 and sternum 8 (Fig. 2: S7, S8), have received little attention in *Hylaeus* taxonomy. They are usually small and only weakly sclerotised. Sternum 7 consists of a basal pair of legs connected by a usually short shaft with paired basal and apical lobes. Sternum 8 is one-piece, sometimes only rhombic; distally various shapes of lobes may form. Two facts are remarkable about these sterna: in their design they appear to be unconstrained and not subjected to formative selection pressure, so that their appearance is not infrequently downright luxury; this also means they remain similar within kinship groups.

How this morphological complex functions is not known in detail. A lock and key principle between partners of the same species cannot be substantiated, because on the female side there are no equivalents in the genital. The actual species recognition apparently occurs via chemical markers, which, according to previous observations, are mediated between the antennae of the females and sensory structures of the scape and the paraocular area of the males (Torchio 1984, Dathe 2009, Erbe 2011). Méhelÿ (1935) discussed in detail the possible functions of the parts of the copulatory apparatus. They are not inserted into the female anal aperture, but essentially only used for external fixation of the partner. Some male parts may serve to protect against the female´s sting apparatus, so that the membranous penis can be inserted and guided.

Bertsch & Titze (2019) describe a similar situation in bumblebees (*Bombus*): "*Although adequate explanations for the morphological diversity of male genital capsule structure remain to be determined, they are obviously conservative characteristics, in which phylogenetically older adaptations have been preserved, probably because selection pressure is low*." The authors know similar phenomena in botany: pollen grains show a variety of adaptations that cannot be explained functionally.

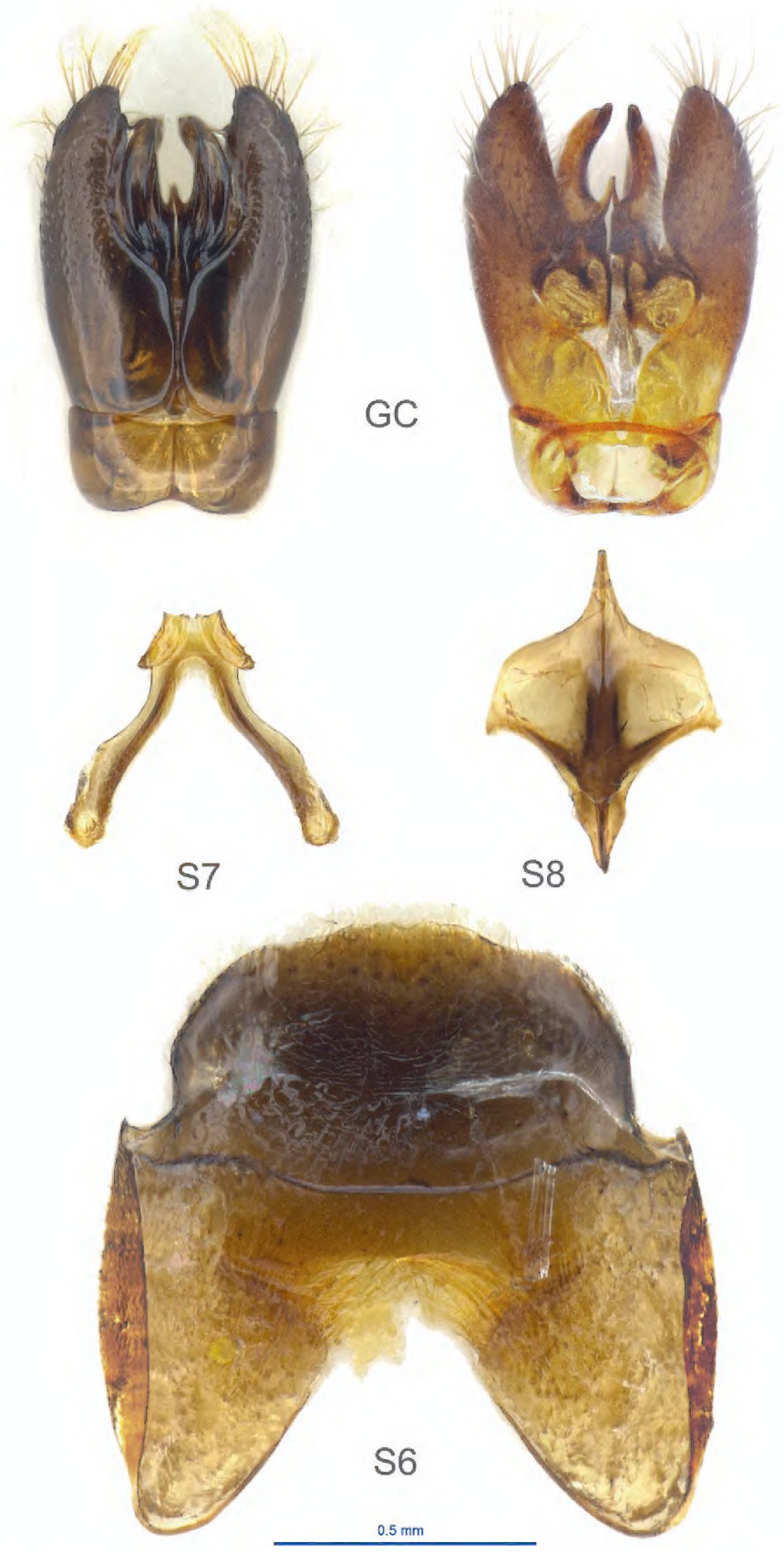
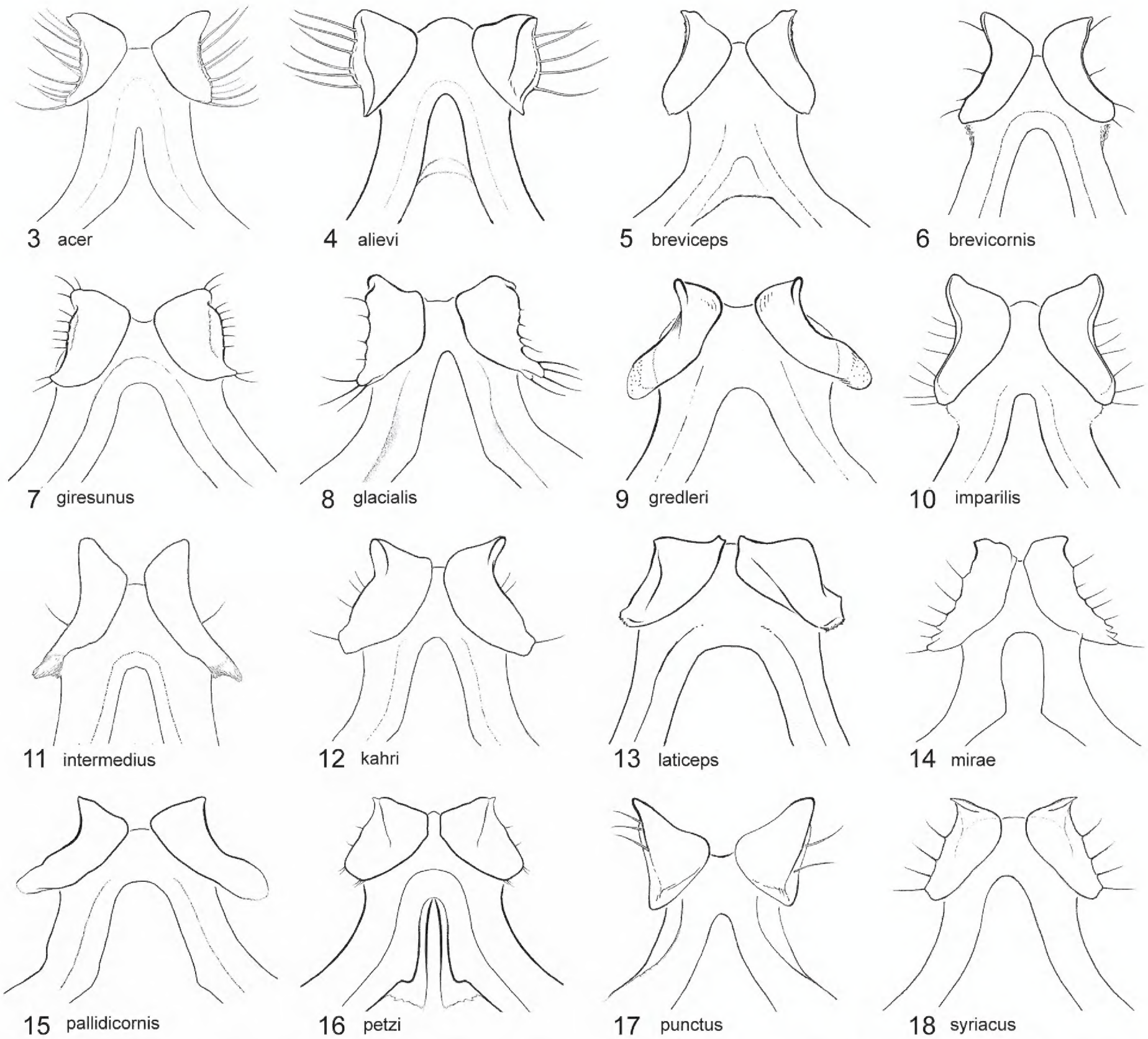
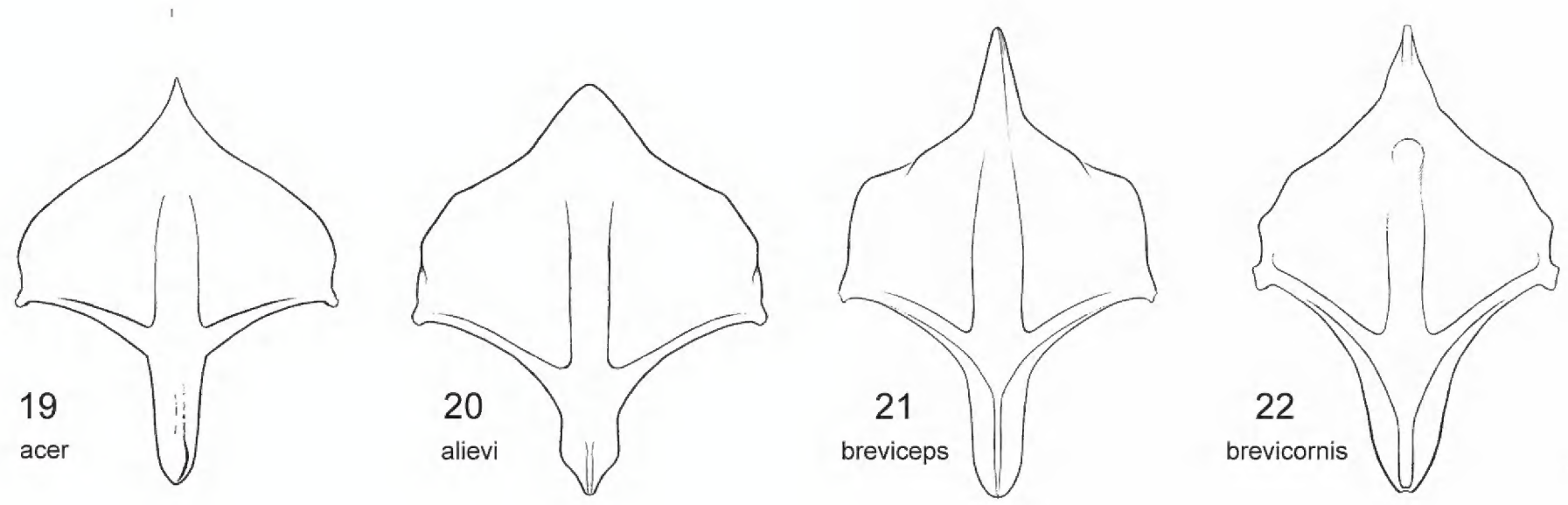



**Fig. 2**: *Hylaeus kahri* ♂, Terminalia: GC – genital capsule, dorsal view left, ventral view right. S6–S8 – sterna 6 to 8. – Scale bar: 0.5 mm.

These are considered phylogenetically conservative and are therefore suitable for the taxonomic classification of genera. Even in *Hylaeus* species, which are morphologically rather monotonous, phylogenetic relationships are apparently preserved in the structure of the terminalia, on the basis of which Méhelÿ (1935) for the first time established a conclusive subgeneric classification within the genus *Hylaeus*. He found „*das männliche Begattungsorgan samt den mit demselben zusammenhängenden Sterniten* [als] *Artcharaktere erster Ordnung*" (ibid. p. 109). Constantinescu (1973, 1974) also recommended using the genital armatures of *Hylaeus* species in taxonomic studies. Popov (1939) gave formal expression to Méhelÿ's system according to the international nomenclatural rules, the main features of which remain virtually unchanged now, 80 years later.




**Figs 3–18**: Male sternum 7 of the *Hylaeus* (*Dentigera*) species, ventral view. **3** – *acer*, **4** – *alievi*, **5** – *breviceps*, **6** – *brevicornis*, **7** – *giresunus*, **8** – *glacialis*, **9** – *gredleri*, **10** – *imparilis*, **11** – *intermedius*, **12** – *kahri*, **13** – *laticeps*, **14** – *mirae* **spec. nov.**, **15** – *pallidicornis*, **16** – *petzi*, **17** – *punctus*, **18** – *syriacus*. – In comparison, not to scale; scale bar 0.1 mm. The genital preparations pictured in Figures 3–50, 56–59, 61 and 62 belong to specimens of the following origin: *acer*: Iran, Elburs – *alievi*: Azerbaijan, Nakhichevan – *biarmicus*: Morocco, Bhalil – *breviceps*: Tajikistan, Zeravshan – *brevicornis*: Austria, Vienna – *chukar*: Turkey, Hakkari – *giresunus*: Turkey, Erzurum – *glacialis*: Switzerland, Engadin – *gredleri*: Austria, Vienna – *gutichauris*: Nepal, Gutichaur – *imparilis*: Austria, Vienna – *intermedius*: Austria, Vienna – *kahri*: Azerbaijan, Nakhichevan – *kaigaunis*: Nepal, Kaigaun – *kashmirensis*: Nepal, Jumla – *kumari*: Nepal, Simikot – *laticeps*: Tajikistan, Zeravshan – *mirae*: Lebanon, Deir Koubel – *pallidicornis*: Kyrgystan, Afleatum – *petzi*: Tajikistan, Dushanbe – *punctus*: Bulgaria, Sandansk – *syriacus*: Israel, Revadim.




**Figs 19–34**: Male sternum 8 of the *Hylaeus* (*Dentigera*) species, ventral view. **19** – *acer*, **20** – *alievi*, **21** – *breviceps*, **22** – *brevicornis*, **23** – *giresunus*, **24** – *glacialis*, **25** – *gredleri*, **26** – *imparilis*, **27** – *intermedius*, **28** – *kahri*, **29** – *laticeps*, **30** – *mirae* **spec. nov.**, **31** – *pallidicornis*, **32** – *petzi*, **33** – *punctus*, **34** – *syriacus*. – In comparison, not to scale.

**Figs 35–50**: Male genital capsule of the *Hylaeus* (*Dentigera*) species, dorsal view. **35** – *acer*, **36** – *alievi*, **37** – *breviceps*, **38** – *brevicornis*, **39** – *giresunus*, **40** – *glacialis*, **41** – *gredleri*, **42** – *imparilis*, **43** – *intermedius*, **44** – *kahri*, **45** – *laticeps*, **46** – *mirae* **spec. nov.**, **47** – *pallidicornis*, **48** – *petzi*, **49** – *punctus*, **50** – *syriacus*. – Scale bar: 0.5 mm.

### *Hylaeus* / subgenus *Dentigera* Popov, 1939

*Prosopis* (*Dentigera*) Méhelÿ, 1935: 45/151. – invalid due to lack of designation of a type species.

*Prosopis* (*Dentigera*) Popov, 1939: 168. – Type species: *Hylaeus brevicornis* Nylander, 1852, by original designation.

### 1. *Hylaeus* (*Dentigera*) *acer* Dathe, 1980

*Hylaeus* (*Dentigera*) *acer* Dathe, 1980: 80–81, 86 ♂♀. Iran: Elburs, Damavand. Holotype ♂, ZMB Berlin. – Özbek & Dathe 2020: 294.

*Prosopis* (*Nesoprosopis*) *acra* (Dathe, 1980) – Warncke 1992: 771.

**Characters**: Head short (HL:HW 0.91), mask ivory-white, shiny; basal area of propodeum with longitudinal ridges in both sexes. Scapes of males strongly thickened (ScL:ScW 1.42), basal part of supraclypeal area almost square; metasoma S3 with pointed process. Stable characters are the balloon-like scapes and the shape of the male terminalia: apical lobes of S7 (Fig. 3) crescent-shaped in outline, laterally with long bristles; in this only similar to *H. alievi*, but bristles in greater number, ca. 8–10. S8 (Fig. 19) also specific: lobus broad, distally very short but pointed, spiculum long with large erect lamella. The genital capsule (Fig. 35) shows in dorsal view penis valves only slightly bent to the side; the dorsal surfaces of the valves are widest at the base.

**Distribution**: The first finds are from Elburs and occurrence of the species is possibly restricted to this area. Later reports from Turkish provinces (Özbek & Dathe 2020: 294) actually belong to *H. alievi*, these specimens do not show the typical pattern of longitudinal ridges on the basal area of the propodeum.

### 2. *Hylaeus* (*Dentigera*) *alievi* Dathe & Proshchalykin, 2021

*Hylaeus* (*Dentigera*) *alievi* Dathe & Proshchalykin, 2021: 171–173 ♂. Azerbaijan: Nakhichevan Aut. Republic. Holotype FSCV Vladivostok.

**Characters**: Small species with short head (HL:HW 0.84), mask white, dull; basal area of propodeum in both sexes with wrinkled meshes, male with strongly thickened scapes (ScL:ScW 1.33), basal area of supraclypeal area trapezoidal, distinctly broader below, S3 with broad bipartite callus. Female with pale apical spot on the scapes.
Terminalia of male similar to *H. acer*, but clearly different in detail (Figs 4, 20, 36): Apical lobes of S7 triangular in outline, laterally with fewer but equally conspicuously long bristles (not all 6 are always well visible). S8 with broad lobe, distally short and blunt, spiculum normally short, without large vertical lamella. Genital capsule has narrower penis valves; dorsal surfaces of valves not wider at base than in middle.

#### Description of the female

Fig. 51

**Diagnosis:** The males were described from Azerbaijan, but in the meantime both sexes have become known from Iran too, so that the female can be added here. The *Hylaeus alievi* female is conspicuous because of its complete light-yellow mask, and the yellow apical spot on the black scapes. The mesopleura are strongly but shallowly punctate. Similarly, unusual is the finely shagreened and only very sparsely punctate sculpture of the T1. These peculiarities make the species unmistakable.

**Female new:** N = 3. TL 5.2–5.8 (5.52) mm, WL 3.3–3.6 (3.47) mm.

**Head**: Proportions HL:HW 0.83–0.89 (0.86), UHW:LHW 1.38–1.45 (1.42), outline transversal-trapezoid. Pilosity short and sparse. Scapes black, at the tip with a yellow spot extending downwards; flagella blackened above, yellow below, terminal segment dark brown.

Mask complete, pale yellow, dull, lateral spots extended to foveae faciales, well beyond scape bases. Foveae faciales long, reaching the vertex. Clypeus CL:CW 0.97–1.00 (0.99), flat; surface finely shagreen, matt, with shallow, sparse punctation, anterior margin, seams und tentorial pits black; supraclypeal area likewise completely yellow. Frons and vertex without gloss, surface streaky-wrinkled with rows of flat, close punctation; vertex coarsely and densely punctate. Genae finely longitudinally striped, with moderately scattered punctation; occiput rounded; malae narrow. Labrum black, with flat horseshoe-shaped hump; mandibles trifid, black, in front of the tip with brown ring.

**Mesosoma** normal, somewhat depressed; pilosity reduced, with erect, short, white hairs, also on underside. Coloration black, pronotum with yellow band, calli totally, tegulae partly yellow. Mesonotum and scutellum shagreen, scarcely glossy, punctation strong, close; mesopleura with punctation somewhat coarser than mesonotum, but remarkably shallow; anterior margin (omaulus) rounded. Legs from the tip of the femur yellow, tibiae with black spot, all basitarsi yellow-white, remaining tarsomeres blackened; wings slightly brownish, venation light brown, subcosta dark. Propodeum evenly rounded, only the terminal area ventrolaterally sharp-edged; medial area basally with mesh row, distally with sharp longitudinal wrinkles; lateral areas finely meshed, matt; terminal area shagreen, surface in the middle somewhat impressed, propodeal furrow narrow with sharp margins.

**Metasoma** spindle-shaped, coloration black. T1 finely shagreen, with fine, very scattered punctation, silky shiny; T2 and following terga more finely and densely punctate; lateral parts of terga with narrow ciliar fringes. End fringe yellowish.

**Fig. 51**: *Hylaeus* (*Dentigera*) *alievi* Dathe & Proshchalykin, 2021, female new. **a** – face, **b** – mesonotum, **c** – mesopleuron, **d** – propodeum and metasoma base. – Scale bar: 0.5 mm.

**Material examined**: 1 ♂, 3 ♀♀ Iran: Ardabil, 20 km S Khalkhal Gollijeh, 1900 m, 20.07.2004, H. Mühle leg., coll. SDEI.

**Distribution**: Azerbaijan: Nakhichevan AR, Shakhbuz, Sharur; Turkey: Hakkâri, Siirt, Tunceli; Iran: Ardabil. The Iranian province of Ardabil lies south of the locus typicus and borders directly on Azerbaijan.

### 3. *Hylaeus* (*Dentigera*) *breviceps* Morawitz, 1876

*Hylaeus breviceps* Morawitz, 1876: 288 ♂. Tajikistan: Saravshan valley. Lectotype (Warncke 1981: 155), ZMMU Moscow.

*Hylaeus bivittatus* Morawitz, 1876: 289 ♀. Tajikistan: Iskander-kul. Lectotype (Warncke 1981: 155), ZMMU Moscow. – Syn. Dathe & Proshchalykin 2017: 14.

*Prosopis breviceps* (Morawitz) – Dalla Torre 1896: 17; Alfken 1936b: 385, 387–388; Popov 1949: 689.

*Prosopis brevicornis* (Nylander, 1852) – Warncke 1981: 155.

*Hylaeus* (*Dentigera*) *breviceps* Morawitz, 1876 – Dathe & Proshchalykin 2017: 14–15; Proshchalykin & Dathe 2021: 174.

**Characters**: Characters of males are the short, broad head (HL:HW 0.85–0.88) and slender conical scapes (ScL:ScW 1.80); their ventral callus on S3 is bipartite, somewhat raised only in large specimens, reduced to paired tubercles in smaller ones. Terminalia Figs 5, 21, 37. Lobes of S7 broader in apical part, their lateral margin without bristles. S8 apically acute, with raised keel.

Females have a transversely elliptical head outline, distinctly broader than high (HL:HW 0.83–0.86), the white spots on the paraocular areas are narrow and situated below the eye margin.

**Distribution**: Russia: Dagestan. Armenia: Erevan. Azerbaijan: Nakhichevan AR (Proshchalykin & Dathe 2021: 174). Central Asia: Kazakhstan; Uzbekistan; Kyrgyzstan; Turkmenistan; Tajikistan (Dathe & Proshchalykin 2018: 22). Northeast China: Xinjiang Province (Proshchalykin & Dathe 2018: 578). The species is widespread in the mountains up to 2000 m altitude.

### 4. *Hylaeus* (*Dentigera*) *brevicornis* Nylander, 1852

*Hylaeus brevicornis* Nylander, 1852: 95 ♀♂. Sweden: Småland. Lectotype ♀ (Erlandsson 1981; see also Nilsson 2007: 170), NHRM Stockholm.

*Prosopis brevicornis* (Nylander, 1852) s. str. – de Beaumont 1958: 166; Benoist 1959: 86 (as *P. brevicornis* "Schenck"); Leclercq 1964: 50.

*Prosopis* (*Nesoprosopis*) *brevicornis* (Nylander, 1852) – Warncke 1972: 764; 1981: 155; 1992: 767.

*Prosopis* (*Dentigera*) *brevicornis* (Nylander, 1852) – Méhelÿ 1935: 151, Tab. XIX, 1-2; Constantinescu 1974: 196, Fig. 1.

*Hylaeus* (*Dentigera*) *brevicornis* Nylander, 1852 – Dathe 1980a: 239; Erlandsson 1981: 177; Aliev 1986: 264; Rasmont et al. 1995: 24; Schwarz et al. 1996: 11; Nilsson 2007: 170; Dathe et al. 2016: 16; Schoder 2018.

*Hylaeus discretus* Förster, 1871: 942–943 ♂. Belgium: Huy Maas. Holotype mono (Dathe 1980: 239), ZSS Munich.

*Prosopis minuta* sensu Alfken, 1905 ff, nex *Apis minuta* Fabricius, 1793.

A serious reappraisal of the numerous synonyms of *H. brevicornis* remains outstanding. All types would need to be reviewed and reassigned, but it is unlikely to result in taxonomic or nomenclatural changes. In particular, Förster's taxa (1871), which were designed according to only one female, are problematic. The names are

*Hylaeus ambiguus* – holotype (mono) ♂ Chur, storage location unknown

*Hylaeus assimilis* – holotype (mono) ♀ Aachen, ZSS Munich

*Hylaeus atratulus* – holotype (mono) ♀ Ungarn, ZSS Munich

*Hylaeus brevipalpis* – 2 syntypes ♀ Wien, ZSS Munich

*Hylaeus carbonarius* – syntypes ♀ Laibach, Piesting, ZSS Munich

*Hylaeus confinis* – holotype (mono) ♀ Wien?, ZSS Munich

*Hylaeus medullitus* – syntypes ♂ ♀ Grenoble, MNHN Paris?

*Hylaeus rotundatus* – holotype (mono) ♀ D?, ZSS Munich

*Hylaeus suspectus* – holotype (mono) ♀ Chur, storage location unknown.

Therefore, lists of synonyms of *H. brevicornis* as well as of *H. imparilis*, *H. intermedius* and *H. kahri* are here largely omitted. The types of the Förster species names used have been re-examined.

**Characters**: Head in both sexes trapezoidal, about as high as wide in outline. Frons shiny in the middle, with scattered punctation. Male scape expanded (ScL:ScW ca. 1.4–1.6), if with yellow marking, then as a lateral stripe. S3 with a pair of small tubercles.
Terminalia Figs 6, 22, 38. Lobes of S7 approximately crescent-shaped in outline, somewhat extended proximally, here with some longer bristles, at the upper margin a few short bristles.

**Distribution**: Morocco, all Europe to 64°N. Caucasus: Ciscaucasus, Azerbaijan, Georgia (Proshchalykin & Dathe 2021: 182). Asia Minor (Özbek & Dathe 2020: 295). South Siberia (Proshchalykin & Dathe 2016: 302). Kazakhstan (Dathe & Proshchalykin 2018: 23).

### 5. *Hylaeus* (*Dentigera*) *giresunus* (Warncke, 1992)

*Prosopis* (*Nesoprosopis*) *glacialis giresuna* Warncke, 1992: 770–771 ♀♂. Turkey: Hakkâri, Varegös. Holotype ♀, OLM Linz.

*Hylaeus* (*Dentigera*) *giresunus* (Warncke, 1992) – Özbek & Dathe 2020: 296, Fig. 3.

**Characters**: In female head with very thickened genae, these wider than compound eyes; clypeus broadly depressed, anterior margin upturned, middle V-shaped raised, smooth; surface with long protruding bristles; lower part of supraclypeal area convex, above broad and flowing into frons; T1 only extremely finely shagreen, shiny, with fine sparse punctation.
Terminalia of a male paratype see Figs 7, 23, 39; apical lobes of S7 on lateral margin with rather regularly arranged short bristles.
Warncke (1992: 771) only mentions as a distinguishing feature of the males of *H. giresunus* and *H. glacialis* that the punctation of the thorax and T1 is somewhat stronger and more scattered. Such characters actually fall completely within the range of normal variability, while the female is totally different from *H. glacialis*. Since he collected the male paratype examined here in the same area and on the same day, but at a different altitude (the holotype female at 1650 m, the paratype male at 2400 m), the doubt expressed by Özbek & Dathe (2020: 297) as to whether the sexes are correctly associated, is not yet dispelled.
In any case, however, the definition of the species, which is tied to a female, holds. A status as a subspecies of *H. glacialis* can be ruled out.

**Distribution**: Turkey: Hakkâri, Erzurum. Montane species, 1700–2400 m.

### 6. *Hylaeus* (*Dentigera*) *glacialis* Morawitz, 1872

*Hylaeus glacialis* Morawitz, 1872: 379–380 ♂. Italy: South Tirol, Trafoi, Franzenshöhe. Holotype by monotypy, ZISP St. Petersburg.

*Prosopis glacialis* (Morawitz, 1872) – de Beaumont 1958: 166; Leclercq 1964: 44.

*Prosopis* (*Nesoprosopis*) *brevicornis glacialis* (Morawitz, 1872) – Warncke 1972: 765; 1992: 767.

*Hylaeus* (*Dentigera*) *glacialis* Morawitz, 1872 – Dathe 1980a: 238; Rasmont et al. 1995: 24; Dathe et al. 2016: 15.

**Characters**: Scapes of males strongly thickened, expanded similarly to *H. kahri*, Sc:ScW 1.3; vertex and genae distinctly narrower than in female of *H. giresunus*; frons

in scape area with small smooth, punctate areas; clypeus depressed basally (along with entire median face), convex distally, anterior margin with ca. 6 protruding bristles; T1 finely shagreen, with strong close punctation. S3 with flat two-part callus. Terminalia Figs 8, 24, 40; apical lobes of S7 narrowly extended proximally and here with longer bristles; lateral margin with few short bristles.
Face of female trapezoidal, slightly converging downward, flattened in middle; anterior margin of clypeus strongly impressed, with protruding row of bristles on impression. Terminal area of propodeum with finely granulated sculpture. T1 only very finely shagreen, with shallow fine sparse punctation.

**Distribution**: Disjunct distribution in high mountainous areas of Europe and Asia Minor, from the Pyrenees to Hakkâri (1500–2400 m).

### 7. *Hylaeus* (*Dentigera*) *gredleri* Förster, 1871

*Hylaeus gredleri* Förster, 1871: 944–946 ♂♀. Austria: Tirol, Telfs. Syntypes, ZSS Munich.
*Hylaeus fumipennis* Förster, 1871: 946–947 ♂. Germany: Aachen. Syntypes, ZSS Munich.
*Hylaeus brevipalpis* Förster, 1871: 1041–1042 ♀. Austria: Vienna. 2 syntypes, ZSS Munich.
*Hylaeus confinis* Förster, 1871: 1043–1044 ♀. Austria: Vienna(?). Holotype by monotypy, ZSS Munich.
*Hylaeus rotundatus* Förster, 1871: 1044–1045 ♀. Germany: Aachen(?). Holotype by monotypy, ZSS Munich.
*Prosopis brevicornis* (Nylander, 1852) – Alfken 1905: 114.
*Prosopis brevicornis sardoa* Alfken 1934: 23 ♀♂. Italy: Sardinia, Cagliari, Iglesias. Holotype ♂, ETH Zurich.
*Prosopis* (*Nesoprosopis*) *brevicornis brevicornis* (Nylander, 1852) – Warncke 1972: 764.
*Prosopis gredleri* Förster, 1871 – de Beaumont 1958: 166; Leclercq 1964: 44.
*Hylaeus* (*Dentigera*) *gredleri* Förster, 1871 – Dathe 1980a: 239; Rasmont et al. 1995: 24; Schwarz et al. 1996: 14; Proshchalykin & Dathe 2016: 304; Dathe & Proshchalykin 2018: 23.
?*Hylaeus parvulus* Janvier, 1972: 113–114 ♂♀. France: Île d'Oléron. Holotype ♂, MNHN Paris (holotype not found – Dathe et al. 2012: 14).

**Characters**: *Hylaeus gredleri* und *H. brevicornis* were long considered a reason for the indivisibility of the superspecies "*H. brevicornis* auctorum" due to their morphological similarity and comparable distribution. Both species are common and often live syntopically. The difference, however, becomes clear when they are compared without the aforementioned prejudice: *H. gredleri* has coarser integument sculpture, which appears correspondingly dull, for example on the frons, whereas these areas are only sparsely punctate and shiny in *H. brevicornis*. This applies to both sexes. The scapes of the males are similarly expanded and spherical, index ScL:ScW 1.4–1.6, but have a different coloration: the pale marking is at the tip of the scape in *H. gredleri*, in *H. brevicornis* at the sides. The light coloration, for example of the pronotum, tends to be more pronounced in *H. gredleri*. These features are by no means present "with all transitions". On the contrary, they prove to be quite stable, especially considering the generally small differences in the brevicornis group. Incidentally, these taxa were widely separated in the recent molecular genetic analyses: they are not even, as might have been suspected, sister species (BOLD 2011, Schmidt et al. 2015, Schoder 2018).
A comparison of the terminalia emphatically confirms the differences (Figs 9, 25, 41). In *H. gredleri* the apical lobes of S7 are clearly longer proximally, the terminal part is hyaline. Only in two specimens could I detect a single short bristle at the margin. S8 differs by having a comparatively long narrow spicule.
Long white stripes along the orbits are characteristic of the female face.

**Distribution**: Found throughout Europe, western Siberia, east to Kazakhstan; south from Morocco to Sicily and the Aegean.

### 8. *Hylaeus* (*Dentigera*) *imparilis* Förster, 1871

*Hylaeus imparilis* Förster, 1871: 1033–1035 ♂. Southern France. Holotype by monotypy, ZSS Munich.
*Hylaeus exaequatus* Förster, 1871: 1035–1036 ♂. Southern France. Holotype by monotypy, ZSS Munich.
*Prosopis brevicornis* auct. partim – Alfken 1905: 121.
*Prosopis brevicornis* var. *imparilis* (Förster, 1871) – Móczár 1960: 9.17.
*Hylaeus brevicornis* var. *imparilis* Förster, 1871 – Meade-Waldo 1923: 18.
*Prosopis* (*Dentigera*) *brevicornis* var. *imparilis* (Förster, 1871) – Méhelÿ 1935: 152, Tab. XIX, 3.
*Prosopis brevicornis* (Nylander, 1852) – Leclercq 1964: 44.
*Prosopis* (*Nesoprosopis*) *brevicornis* (Nylander, 1852) – Warncke 1972: 764.
*Hylaeus* (*Dentigera*) *imparilis* Förster, 1871 – Dathe 1980: 240; 1980a: 84; 1996: 14; Rasmont et al. 1995: 24; Dathe et al. 2012: 56; 2016: 17, 44; Schoder (2018); Lhomme et al. 2020: 67; Proshchalykin & Dathe 2021: 174.

**Characters**: A dainty species with distinctive pale coloration. It is particularly common in the Mediterranean region and further east and varies accordingly in head shape, coloration and punctation. The scapes of the males are slenderly spheroidal with straight lateral edges and usually a pale apical spot, scape index ScL:ScW 1.8–2.0. The genae are narrow. Meso- and metasoma strongly punctate, usually with distinct ribs and edges of propodeum.
Male terminalia (Figs 10, 26, 42): apical lobes of S7 curved bean-shaped in profile, with well-defined row

of bristles on lateral outer margin; apex of S8 blunt and broadened.
In females the paraocular area is often completely filled with pale (white to light yellow) marks.

**Distribution**: Circum-Mediterranean, southern and central Europe, Middle East, Asia Minor, Caucasus, Iran.

### 9. *Hylaeus* (*Dentigera*) *intermedius* Förster, 1871

*Hylaeus intermedius* Förster, 1871: 943–944 ♂. Poland: Ratibor/Oberschlesien (Racibórz/Śląsk). Holotype by monotypy, ZSS Munich.
*Prosopis intermedia* (Förster, 1871) – Dalla Torre 1896: 25.
*Prosopis brevicornis* (Nylander, 1852) – Alfken 1905: 114.
*Prosopis* (*Nesoprosopis*) *brevicornis* (Nylander, 1852) – Warncke 1972: 764.
*Hylaeus brevicornis* Förster, 1871) – Meade-Waldo 1923: 18; Leclercq 1964: 44.
*Hylaeus* (*Dentigera*) *gredleri* Förster, 1871 – Dathe 1980: 239; 1996: 14.
*Hylaeus* (*Dentigera*) *intermedius* Förster, 1871 – Dathe et al. 2016: 16, 44; Schoder 2018; Özbek & Dathe 2020: 299; Proshchalykin & Dathe 2021: 174.

**Characters**: Förster (1871: 943) had chosen the name with care, because in essential characters *H. intermedius* stands between *H. gredleri* and *H. kahri*. He himself compared the single male in his possession with *H. fumipennis* Förster (= *H. gredleri* Förster) and observed differences mainly in the scattered punctation on frons and vertex, and the central furrow widened above in the finely shagreen and shiny terminal area. The scape of the male is conical, only slightly expanded (ScL:ScW 1.7–1.8), the sides straight, the apex marked yellow. The white mask appears shield-like because the markings on the anterior margin of the clypeus are connected to the lateral spots.
Male terminalia (Figs 11, 27, 43): apical lobes of S7 extended proximally and ending in a membranous appendix; lateral margin with a longer bristle. S8 narrower in outline and with elongated spicule.

**Distribution**: Mainly found in the countries around the Mediterranean and the Black Sea. Known in central Europe from Poland and Austria.

**Remarks**: In several collections, male specimens with slender scapes were found, which in their other characters reminded of *H. kahri* or *H. gredleri*; however, they were clearly larger than the latter, the genae broadened and S3 with a small pair of tubercles. In a sense, they were "intermediate" to the compared species. We have tentatively treated a taxon *H. intermedius* Förster as valid (species revocata) in a determination table (Dathe et al. 2016), but are aware that a reliable determination based on morphological characters alone continues to be very problematic – unless one has these species present side by side. The study by Schoder (2018) recently supported this approach with the molecular genetic definition of the females. For the animals determined as «intermedius», she identified two clearly separate clades, one clustering close to *H. gredleri*, the other to *H. kahri*. Possibly a cryptic species is involved here, or this is *H. kahri* itself. Her morphological examinations also revealed a specific pattern of variation in the selected indices of the heads for *H. intermedius*.

### 10. *Hylaeus* (*Dentigera*) *kahri* Förster, 1871

*Hylaeus kahri* Förster, 1871: 954–956 ♂. Austria: Steiermark(?). Holotype by monotypy, ZSS Munich.
*Hylaeus carbonarius* Förster, 1871: 1045–1046 ♀. Slovenia: Laibach [Ljubljana]. Syntypes, ZSS Munich.
*Hylaeus assimilis* Förster, 1871: 1046–1047 ♀. Germany: Aachen. Holotype by monotypy, ZSS Munich.
*Prosopis* (*Dentigera*) *kahri* (Förster, 1871) – Méhelÿ 1935: 152, Tab. XIX, 5–8.
*Prosopis kahri* Förster, 1871 – de Beaumont 1958: 166.
*Prosopis brevicornis* var. *kahri* (Förster, 1871) – Móczár 1960: 9.29.
*Prosopis brevicornis* (Nylander, 1852) – Alfken 1905: 114; Leclercq 1964: 45; Warncke 1972: 764.
*Hylaeus* (*Dentigera*) *kahri* Förster, 1871 – Dathe 1980a: 80; 1980b: 236–238; Rasmont et al. 1995: 24; Dathe et al. 2016: 16, 45; Özbek & Dathe 2020: 300; Boustani et al. 2021: 15; Proshchalykin & Dathe 2021: 175.

**Characters**: Male scapes strongly expanded, ScL:ScW 1.3–1.4, with curved lateral edges; flagellum recessed decentrally, forming a free, deeply depressed area inwards; outer margin of scape with yellow markings, triangularly tapering proximally. S3 in normal-sized specimens with strong triangular cusp. Integument in both sexes shagreen with moderate to strong, close punctation, but largely silky-glossy. Females are also richly pale-marked, with extensive yellow-white spots on the paraocular areas and often also on the clypeus.
Male terminalia (Figs 12, 28, 44): apical lobes of S7 long oval, convex distally; lateral margin with few short bristles. S8 with distinct spiculum.

**Distribution**: Western Europe to the Caucasus, Asia Minor and Iran, mainly in the Mediterranean riparian areas and on the Black Sea. In the Alps up to 1600 m altitude, north to southern Germany (Rhineland-Palatinate).

### 11. *Hylaeus* (*Dentigera*) *laticeps* Morawitz, 1876

*Hylaeus laticeps* Morawitz, 1876: 291 ♀. Uzbekistan: Shakhimardan. Holotype by monotypy, ZMMU Moscow. – Meade-Waldo 1923: 20.
*Prosopis laticeps* (Morawitz, 1876) – Dalla Torre 1896: 26.

*Prosopis brevicornis* (Nylander, 1852) – Warncke 1981: 155.

*Hylaeus nigritarsis* Morawitz, 1876: 288–289 ♂. Tajikistan: Sarafshan. Lectotype ZISP St. Petersburg. – Syn. Dathe & Proshchalykin 2017: 25.

*Hylaeus* (*Dentigera*) *laticeps* Morawitz, 1876 – Dathe & Proshchalykin 2017: 25; 2018: 23.

**Characters**: Males are immediately recognisable by the short, broad head (HL:HW 0.86) and the extremely expanded black scapes with a small yellow apical spot (ScL:ScW 1.2–1.3). The mask is white, the upper part of the supraclypeal area is strikingly raised. Abdominal callus on S3 narrowly triangular, sharp and medio-apically incised.

Male terminalia Figs 13, 29, 45. Lobes of S7 appear more or less triangular-compact, their outer lateral margin without bristles. S8 apically acute, with keel-like arch, the spiculum narrow. Females have a transversely elliptical head outline, distinctly broader than high (HL:HW 0.83–0–86), the white spots on the paraocular areas are very extensive and extend upwards far beyond the scape bases.

**Distribution**: Central Asia: Kazakhstan; Uzbekistan; Turkmenistan; Tajikistan (Dathe & Proshchalykin 2018: 23–24).

### 12. *Hylaeus* (*Dentigera*) *luna* Chen & Xu, 2009

*Hylaeus* (*Dentigera*) *luna* Chen & Xu, 2009: 35–36 ♂♀. China: Hubei, Shenlongjia [Shennongija] Natn. Res. Holotype ♂, MCAU Beijing.

**Characters**: Unfortunately, the types were not borrowed, so that only the original description can be reproduced here. The head is broader than high (HL:HW 0.91); the scapes are expanded (ScL:ScW 1.46), black with a broad yellow stripe along their entire length. Propodeum lacks transverse and oblique propodeal carinae. S3 of metasoma with two weak protuberances.

Terminalia see Figs 7–14 in Chen & Xu (2009: 38–39). The apical lobes of S7 are shown as compact kidney-shaped, without bristles. The female paratype has only small white lines at the lower edge of the compound eyes. Structurally it resembles the male.

The describing authors compared the species with *Hylaeus brevicornis*; however, as their illustrations suggest, the sculpture of the face above the antennal bases is clearly coarser, reminiscent of *Hylaeus gredleri*.

**Distribution**: China: Hubei province, Shennongjia National Nature Reserve. Thus, the brevicornis group is recorded in China east to 110°41'E.

### 13. *Hylaeus* (*Dentigera*) *mirae* spec. nov.

urn:lsid:zoobank.org:act:4ACDE979-96A2-4D60-B500-B11FA26F9FA1

**Diagnosis**: The males of the new species are characterised by completely black scapes with strong punctation. This is particularly remarkable in that these are usually richly pale-marked in species of the region with strongly thickened scapes (*Hylaeus kahri, H. punctus, H. syriacus*). The mask is ivory-white, and in females the clypeus and often the base of the supraclypeal area are also pale-spotted.

**Description: Male** (Fig. 52a–e). N = 10. Total length 4.3–5.1 (4.74) mm, wing length 3.0–3.5 (3.26) mm.

**Head**: Proportions HL:HW 0.93–0.96 (0.94), UHW:LHW 1.48–1.55 (1.51), outline transverse-trapezoid. Pilosity short and sparse. Scapes completely black (only one specimen has a strange vertical yellow line on the center), strongly dilated and pyriform, ScL:ScW 1.24–1.39 (1.31); backside flat, front with fine subcontiguous punctation, matt. Flagella short, blackened above, yellow below. Mask complete, ivory-white, weakly shiny, side patches expanded up to the foveae faciales, far beyond the scape bases. Foveae faciales distinct, reaching the vertex. Clypeus CL:CW 1.19–1.32 (1.26), flat; surface slightly shiny, finely shagreen with shallow, sparse punctation, anterior margin black. Supraclypeal area white, black only on the apical area, transition to the frons gradual. Frons and vertex shiny, with dense moderate punctation, vertex streakily punctate. Genae striated with elongated punctation; occiput rounded; malae narrow. Labrum black, with flat callosity; the bifid mandibles black with brown ring before tips.

**Mesosoma** normal, rounded, somewhat depressed; pilosity reduced, with erect, short, white hairs, also on underside. Coloration black, pronotum with yellow stripe that can be narrowly interrupted in the middle, calli and tegulae nearly totally white. Pronotum not expanded, anterior margin in the middle narrow, dorsolateral angles sloping. Mesonotum and scutellum shagreen, matt, punctation moderate, dense; mesopleura with punctation somewhat coarser and more sparse, omaulus rounded. Legs black, with yellow anterior surface of foretibiae, tips of femora and tibial bases white, all basitarsi and second tarsomeres white; remaining tarsomeres black; wings clear, venation light brown, costa dark. Propodeum evenly rounded; medial area sharply reticulately wrinkled, with rough meshes, surface shagreen, laterally demarcated by a row of meshes; lateral areas finely wrinkled, matt; terminal area with finely sculptured surface, glossy in the middle, propodeal furrow narrow but deep.

**Metasoma** cylindrical, coloration black. T1 shagreen, silky shiny, punctation moderate, subcontiguous; T2 and following terga more finely and densely punctate; lateral parts of terga with narrow ciliar fringes. S3 with shallow bicuspid transverse callus. Terminalia (Figs 14, 30, 46): S7 with apical lobus proximally extended, laterally with

**Fig. 52**: *Hylaeus* (*Dentigera*) *mirae* **spec. nov.** Holotype male: **a** – face, **b** – mesopleuron, **c** – mesonotum, **d** – metasoma base, **e** – metasoma ventral, S3 with bicuspid callus. Paratype female: **f** – face, **g** – mesopleuron, **h** – mesonotum, **i** – metasoma base. – Scale bar: 0.5 mm.

6 indistinct short bristles; S8 narrowly rhombiform, spiculum long, apex formed as a long extended narrow tip; genital capsule normal, gonoforcipes shorter than gonobase; penis valves of *brevicornis* type, in dorsal view shorter than the gonoforcipes.

**Female** (Fig. 52f–i). N = 4. Total length 4.2–4.9 (4.62) mm, wing length 3.1–3.4 (3.28) mm.

**Head**: Proportions HL:HW 0.93–0.95 (0.94), UHW:LHW 1.40–1.43 (1.42), outline transverse-trapezoid. Pilosity short and sparse. Scapes and pedicels black, flagella short, blackened above, yellow below. Mask reduced, ivory-white, matt, side patches expanded up to foveae faciales, far beyond the scape bases. Foveae faciales long, reaching the vertex. Clypeus CL:CW 1.12–1.18 (1.15), flat; surface strongly shagreen, matt, with shallow, sparse punctation, anterior margin black; centrally with large approximately rectangular pale spot, supraclypeal area often basally with two pale dots. Frons and vertex shiny, with dense moderate punctation, vertex streakily punctate. Genae streaked with elongated punctation; occiput rounded; malae narrow. Labrum black, with flat annular cusp; mandibles trifid.

**Mesosoma** normal, rounded, somewhat depressed; pilosity reduced, with erect, short, white hairs, also on underside. Coloration black, pronotum with yellow band, sometimes interrupted in the middle, calli and tegulae nearly totally white. Pronotum hardly expanded, anterior margin narrow in the middle, dorsolateral angles sloping. Mesonotum and scutellum shagreen, matt, punctation moderate, dense; punctation on mesopleura somewhat coarser and more sparse, omaulus rounded. Legs black, with yellow anterior surface of foretibiae, tips of femora and half of tibial base white, all basitarsi black with basal white fleck, remaining tarsomeres black; wings clear, venation light brown, costa dark. Propodeum evenly rounded; medial area sharply reticulately wrinkled, with rough meshes, shagreen, laterally demarcated by a row of meshes; lateral areas finely wrinkled, matt; terminal area with finely sculptured surface, glossy in the middle, propodeal furrow narrow and deep.

**Metasoma** spindle-shaped, coloration black. T1 shagreen but shiny, with punctation moderate, close to sparse; T2 and following terga more finely and densely punctate; lateral parts of terga with narrow ciliar fringes. End fringe yellowish.

**Type material**: 10 ♂♂, 4 ♀♀. Holotype ♂ Lebanon: Mount Lebanon, Deir Koubel near Choueifar, 300 m, 02.07.1995, C.G. Roche legit, coll. SDEI. – Paratypes: Lebanon: 4 ♂♂ data as holotype; 1 ♂ Mount Lebanon, Aley, Ain es Sayde, 15.08.1994; 1 ♂ Mount Lebanon, Monteverde near Mansourieh, 350 m, 25.06.1995; 1 ♂ Baksmaya, Nahr el Jawz, 250 m, 01.06.2001, all leg. C.G. Roche. 1 ♂ 2 ♀♀ Horch Ehden Nature Reserve, 25 km SE Tripoli, 1300–1600 m, 13.–18.09.2000, leg. P.M. Pavett; all coll. SDEI. 1 ♂ 1 ♀ Lebanon North: Hadath el Jebbe, border of cedar forest, 34°13'05"N 35°56'17"E, 1681 m, 22.08.2018, leg. Boustani et Jabbour; 1 ♀ Arz Tannourine, gate area, 34°12'28.3"N 35°55'57.9"E, 1754 m, leg M. Boustani, coll. MBOU.

**Etymology**: The new species is dedicated to Mira Boustani (University of Mons-Hainaut/Belgium) in recognition of her contributions to the knowledge of the bee fauna of her home country, first published in a critical compilation in 2021 (Boustani et al. 2021).

**Distribution**: The species is widespread in the area of the eastern Mediterranean countries and seems to be by no means rare. Until now, however, it has been misinterpreted; I had incorrectly determined it as "*syriacus*". It was possible to revise records from Israel, which are listed here:

Israel: Judean Foothills: 1 ♂ Neve Shalom, ITM 1975, 6365, 14.05.2009, 1 ♂ Har'el, ITM 1948, 6360 29.05.2009, 1 ♂ nr Beit Nir, ITM 1863.6186, 12.06.2009, G. Pisanty leg., 2 ♂♂, 2 ♀♀ Nahshon, ITM 1967, 6376, 08.06.2009, Pisanty et Barta leg.; Kfar Menahem: 1 ♀ 19.05.2011, N. Meltzer leg., 3 ♂♂, 3 ♀♀ 18.03.2018, T. Roth leg.; 1 ♂, 1 ♀ Mishmar David, 09.04.2017, T. Roth leg.; 1 ♂ Tal Shahar, 02.04.2010, G. Pisanty leg.; 1 ♂ Nahal Batra, 32.913°N 35.681°E, 43 m, 23.05.2019, leg. Dorchin et Roth; 1 ♀ 'En Tina NR, 33.084°N 35.642°E, 77 m, 19.06.2019, leg. Dorchin, Sviri et Mersmann; 1 ♀ Nahal Zawitan, Rd. 9088 nr Qazrin, 32.983°N 35.715°E, 349 m, 12.06.2019, Dorchin et Sviri; 4 ♂♂ 2 ♀♀, Moradot, HaGolan Nature Reserve, Nahal Zamud nr Darbashiyya, 33.087°N 35.652°E, 246 m, 19.06.2019, leg. Dorchin, Sviri et Mersmann; 4 ♀♀ Moradot, HaGolan NR, Nahal Neshef, 33.094°N 35.650°E, 184 m, 19.06.2019, leg. Dorchin, Sviri et Mersmann; coll. Steinhardt Museum Tel Aviv.

## 14. *Hylaeus* (*Dentigera*) *pallidicornis* Morawitz, 1876

*Hylaeus pallidicornis* Morawitz, 1876: 290 ♀♂. Uzbekistan: Ferghana, Shakhimardan. Lectotype ♂ (Warncke 1981: 155), ZMMU Moscow; Meade-Waldo 1923: 21; Popov 1951: 164.

*Prosopis pallidicornis* (Morawitz, 1876): Dalla Torre 1896: 29.

*Prosopis* (*Dentigera*) *brevicornis* var. *pallidicornis* (Morawitz, 1876): Méhelÿ 1935: 152, Tab. XIX, 4.

*Prosopis breviceps* auct. nec Morawitz: Alfken 1936b: 385, 387; Popov 1949: 689; Osytchnjuk 1970: 118; Osytchnjuk et al. 1978: 306, 310; Dathe 1980: 241.

*Prosopis sinaitica* Alfken, 1938 ♀. Egypt: Sinai Mountains. Type ZMB Berlin. **Syn. nov.**

*Prosopis* (*Nesoprosopis*) *brevicornis* (Nylander, 1852): Warncke 1981: 155.

*Hylaeus* (*Dentigera*) *pallidicornis* Morawitz, 1876: Dathe 1986b: 35; Dathe & Proshchalykin 2017: 32; Proshchalykin 2017b: 259; Proshchalykin & Dathe 2021: 175.

**Characters**: The special feature of this dainty species is its strikingly bright yellow wing venation, although the stigma can also be light brown. Males resemble *Hylaeus imparilis* with their slender, pale yellow striped scape and the trapezoidal outline of the head; the antennae are very short, S3 has a flat, medially notched callus. Male terminalia (Figs 15, 31, 47): apical lobes of S7 kidney-shaped with dilated proximal part, margin without bristles; S8 apex only short; GC with penis valves laterally and basally only weakly curved, outline rather almond-shaped, the interspace narrow. Females have a completely black face, only rarely with tiny yellow dots on the orbits at the level of the scape bases.

**Distribution**: Primarily known from Central Asia, but widespread from Egypt (Sinai) through the Near East (Lebanon) and Turkey, Azerbaijan, Iran to Mongolia.

### 15. *Hylaeus* (*Dentigera*) *petzi* Dathe & Proshchalykin, 2018

*Hylaeus* (*Dentigera*) *petzi* Dathe & Proshchalykin, 2018: 25–27 ♂♀. Tajikistan: Khatlon Prov., Chimbulak. Holotype ♂, OLM Linz.

**Characters**: This is a small, dainty species with a shiny integument, conspicuous for its comparatively dense and long white pubescence. Male scapes expanded, ScL:ScW 1.54, black with white triangular spot, S3 with flat, blunt-bicuspid transverse callus. Terminalia see Figs 16, 32, 48. S7 with compact rectangular lobes with a few fine bristles on the outer edge.
Females with totally black face; frontal head index HL:HW 0.78 (male 0.86). Anterior surface of clypeus raised in bulge in middle, depressed on both sides; morphology and integument sculpture similar to male.

**Distribution**: Tajikistan.

### 16. *Hylaeus* (*Dentigera*) *punctus* Förster, 1871

*Hylaeus punctus* Förster, 1871: 940–942 ♂ (nec ♀). Croatia: Dalmatia. Syntypes, ZSS Munich.
*Prosopis puncta* (Förster, 1871) – Dalla Torre 1896: 30; Alfken 1905: 113; 1936b: 385.
*Prosopis* (*Nesoprosopis*) *puncta* (Förster, 1871) – Warncke 1972: 765; 1992: 767.
*Hylaeus* (*Dentigera*) *punctus* Förster, 1871 – Dathe 1980: 234–235; Özbek & Dathe 2020: 301.

**Characters**: The species is hard to mistake because of its distinctive sculpture and characteristic mask, at least in the male. Its mask is usually intensely yellow and appears three-pointed because of the wedge-shaped clypeus macula below; scapes strongly expanded, ScL:ScW 1.3–1.4; sternum 3 with strong, anteriorly shallowly hollowed cusp; metasoma dorsally with coarse contiguous punctation. Male terminalia (Figs 17, 33, 49): apical lobes of S7 triangular, margin with few protruding bristles, S8 apical with broad apex, spiculum elongate; GC with narrowed gonoforcipes, penis valves very narrow with only slight interspace. The integument of females is correspondingly strongly sculptured, the paraocular area largely filled, and the clypeus mostly yellow-spotted.

**Distribution**: Balkans, Asia Minor, Near East, Iran.

### 17. *Hylaeus* (*Dentigera*) *syriacus* (Alfken, 1936)

*Prosopis syriaca* Alfken, 1936a: 51–52 ♀♂. Lebanon: Becaa, Said Neil. Holotype ♀, ZMB Berlin.
*Hylaeus* (*Dentigera*) *syriacus* (Alfken, 1936) – Boustani et al. 2021: 17.

**Characters**: This species is close to *Hylaeus kahri*, but is distinguished in the male by an even stronger plastic development of scapes and ventral humps. The scapes are almost as wide as long and also particularly thick, ScL:ScW 1.14–1.25 (*H. kahri* ScL:ScW 1.3–1.4). S3 bears a strong semicircular process directed backwards, depressed in the middle (not bipartite). In both sexes the head is distinctly broader than high (HL:HW ♂ 0.86–0.89, ♀ 0.86–0.89), the genae thickened. However, differentiation from large specimens of *H. kahri* can be difficult. Male terminalia (Figs 18, 34, 50): apical lobes of S7 broadly crescent-shaped, outer margin with 4 (5) fine, regularly arranged bristles; S8 with broad spiculum.
Characteristic of the female is the extensively yellowish-white face, for apart from the large lateral spots, which extend above far beyond the antennal bases and end broadly, the clypeus is also often almost completely pale coloured, and only the sutures below the tentorial pits remain narrowly wedge-shaped black.

**Distribution**: Lebanon, Azerbaijan (Nakhichevan AR).

**Remarks**: It does not seem to be completely excluded that *H. syriacus* and *H. kahri* belong to the same species. However, in Shakhbuz, Zarnatun, both forms live side by side, but no transitional forms occur between them. Genetic sequencing of such specimens would be useful.

## The species of the Himalayas

The following is a compilation of the *Dentigera* species that have been described from the Kashmir region and Nepal. This group shows a certain exclusivity, which probably has to do with the special conditions in high mountains. It is striking that a whole series of species are

so far only known from single specimens and that the sexes cannot always be associated with certainty.
The taxonomic evaluation of many specimens is unusually difficult, especially in the case of the very similar females. Their colour characters are quite uniform; the propodeum is equally rounded, with the basal area only wrinkled at the base and the remaining parts with fine sculpture; tergum 1 has white lateral fringes, it is smooth and shiny, hardly chagreen, the punctation fine and rather scattered. The males possess a slightly larger number of usable morphological characters, but they too give the impression of continuing radiative development. Finally, hybridisation between local forms cannot be excluded, so that the findings recorded here can only be preliminary. Above all, they may serve as an orientation for further investigations, also supported by molecular genetics.
So far, four species have been identified; one of them, *Hylaeus kumari*, was described only recently (Ikudome & Dathe 2021), two others are newly introduced here. The longest known is *Hylaeus kashmirensis* (Nurse, 1903). This species is easily recognisable by its slender black scape and broad head, and it also seems to be more common. The other rarer species have males with thickened black scapes and differ only in subtle details: the shape of the scapes and abdominal humps, in color characters, and in the punctation of the integument.

## 18. *Hylaeus* (*Dentigera*) *kashmirensis* (Nurse, 1903)

*Prosopis kashmirensis* Nurse, 1903: 534–535 ♀♂ (nec ♀). India: Kashmir. Lectotype ♂ (Dathe 2010: 44), NHML London.
*Hylaeus* (*Dentigera*) *kashmirensis* Nurse, 1903 – Dathe 2010: 44; Ikudome & Dathe 2021: 2.
*Prosopis brevicornis* (Nylander, 1852) – Warncke 1981: 157.

**Characters**: This is one of the larger Himalayan species with TL 5.9–6.5 mm. Both sexes have a transversely oval head outline (HL:HW ♂ 0.86–0.89, ♀ 0.85–0.87), the genae are thickened and the propodeum is relatively smoothly sculptured, especially the lateral areas and the adjacent parts of the basal area. Of the species known so far, only the male of *H. kashmirensis* has a slender, entirely black scape (ScL:ScW 1.9–2.1). Terminalia see Fig. 56, apical lobes of S7 in projection bluntly banana-shaped with few bristles.

The females are distinguished by pale yellow, largely filling lateral spots, usually extending upwards beyond the base of the scape. T1 – as in other Himalayan species – basally smooth, only distally somewhat shagreen, with minute to fine scattered punctation; depressions pale.

**Distribution**: India: Kashmir; Nepal: Karnali Province. New records: 1 ♂ Gutichaur river, 29°14'55"N 82°18'48"E, 2620 m, 14.06.1997; 1 ♀ Lamri Umg., 29°20'03"N 82°22'34"E, 15.06.1997; 1 ♀ ibid. 29°16'34"N 82°16'23"E, 2600 m, 21.06.1997; 2 ♂♂ Jumla Talphi, 29°20'03"N 82°22'34"E, 3115 m, 15.06.1997; 1 ♀ Jumla Umg. KF, 26.05.2007; 3 ♀♀ ibid. 29°16'25"N 82°11'32"E, 2450 m, 22.06.1997; 1 ♀ ibid. Flughafen, 23.06.1997; 1 ♂ 4 ♀♀ Simikot ca. 10 km S, Karnali valley, ca. 2200 m, 09.07.2001; all leg. F. Creutzburg, coll. SDEI.

## 19. *Hylaeus* (*Dentigera*) *vetustus* (Nurse, 1903)

*Prosopis vetusta* Nurse, 1903: 536–537 ♀. India: Kashmir, 1500–1800 m. Holotype by monotypy, NHML London.
*Prosopis brevicornis* (Nylander, 1852) – Warncke 1981: 157.
*Hylaeus* (*Dentigera*) *vetustus* (Nurse, 1903) – Dathe 2010: 44–45, Fig. 6.

**Remarks**: *Prosopis vetusta* was described on the basis of a single female, collected right next to *Hylaeus kashmirensis*, but not assigned to this male. The type female has as special features extensive yellow spots on the paraocular areas, also the clypeus is yellow-spotted. Recent collections of small series by Creutzburg (Jena) have created doubts about its status. It could well be a brightly marked specimen of *Hylaeus kashmirensis*, as individual specimens of this species also tend towards having a spotted clypeus. Furthermore, the specimen fits *H. kashmirensis* in size and has the characteristic broad head (HL:HW 0.86). On the other hand, the yellow coloration of the mask speaks against their conspecifity.

*Hylaeus vetustus* also resembles the females of *Hylaeus syriacus* and *Hylaeus alievi* in having an extended yellow mask However, it differs from both by the rhombic shape of the supraclypeal area, which has parallel sides in the latter. Tergum 1 of *H. vetustus* resembles *H. alievi*, for the punctation in both is only very fine and scattered; the integument is smooth and shiny, though in *H. alievi* distinctly shagreen and less lustrous. *H. syriacus* has moderately close punctation. The differences are subtle, but in view of the generally very small differences in the brevicornis group, the combination of characters seems to be very special in each case. – Nurse's (1903) statement "Nearest to *P. strenua*." is incorrect.

## 20. *Hylaeus* (*Dentigera*) *kumari* Dathe & Ikudome, 2021

*Hylaeus* (*Dentigera*) *kumari* Dathe & Ikudome, 2021: 2–4 ♂. Nepal: Bagmati, Dhunche. Holotype by monotypy, ELKU Fukuoka.

**Characters**: This small species (< 5 mm TL) was only recently described from a single male (Ikudome & Dathe 2021) and is still little known. The type is characterised by strongly thickened, pyriform, completely black scapes. T1 with moderately close punctation.

**Fig. 53**: *Hylaeus* (*Dentigera*) *kumari* Dathe & Ikudome, 2021, female new. **a** – face, **b** – mesonotum, **c** – mesopleuron, **d** – propodeum and metasoma base. – Scale bar: 0.5 mm.

**Description of the female**: Fig. 53

**Diagnosis:** The assignment of a female to *Hylaeus kumari* made here is not without problems, because the specimen was taken from another locality which does not directly correspond with those of the two known males. However, it shows similarities with them, and it differs from the females of the other species in certain characters. Future observations should pay attention to whether the sexes occur together.

**Female new**: N = 1. TL 5.15 mm, WL 3.84 mm.

**Head**: Proportions HL:HW 0.89, UHW:LHW 1.48, outline rounded-trapezoid. Scapes black; flagella blackened above, yellow below. Paraocular area ivory-white filled to above antennal sockets, dorsally oblique to foveae faciales, shiny; foveae faciales long, reaching the vertex. Clypeus with white fleck; CL:CW 1.11, flat; surface finely shagreen, matt, with indistinct shallow punctation; supraclypeal area rhombic, with protruding lateral corners. Frons and vertex shiny, moderately densely punctate. Genae finely longitudinally striped, with moderate scattered punctation; occiput rounded; malae narrow. Labrum black, with flat horseshoe hump; mandibles trifid, black, in front of the tip with brown ring.

**Mesosoma** normal, rounded; pilosity with erect white hairs laterally and on underside. Coloration black, pronotum with two long yellow stripes, calli and tegulae pale. Pronotum not expanded, anterior margin medially narrow, dorsolateral angles rounded. Mesonotum, scutellum and mesopleura shagreen, silky-shiny, punctation moderately dense; omaulus rounded. Legs black, only tibia bases yellow; wings clear, venation black, costa dark. Propodeum evenly rounded; basal area with irregular mesh ridges, laterally not demarcated; lateral areas setose, finely shagreen, matt; terminal area with finely sculptured surface, propodeal furrow narrow below, dorsally widely broadening.

**Metasoma** spindle-shaped, coloration black. T1 smooth and shiny, with punctation fine, sparse, apically somewhat denser, with white lateral fringe patches; T2 and following terga more finely and densely punctate; distal margins blanched, with fine ciliary bands. End fringe pale.

**Material examined**: Nepal: 1 ♀ Lamri Umg. 29°20'03"N 82°22'34"E, 15.06.1997; 1 ♂ Karnali, Simikot 14 km NW, Kermi Umg., 30°02'55"N 81°42'20"E, 2800 m, 19.–20.06.2001; all leg. F. Creutzburg, coll. SDEI.

**Distribution**: Nepal.

### 21. *Hylaeus* (*Dentigera*) *gutichauris* spec. nov.

urn:lsid:zoobank.org:act:47161A86-73EF-45C0-B059-E9910630CF6C

**Diagnosis**: The male of the new species has strongly expanded, black scapes with a tiny apical spot; the mask is ivory-white. The female has oval spots in the paraocular area.

**Description: Male** (Fig. 54a–d). N = 1. TL 5.4 mm, WL 3.7 mm.

**Head**: Proportions HL:HW 0.94, UHW:LHW 1.50, outline trapezoidal. Pilosity distinct, long and protruding. Scapes strongly expanded, black, with small yellow dot at the tip, ScL:ScW 1.52; back flat, front evenly domed, without impression, with finely crinkled punctation, matt. Flagella short, blackened above, yellow below. Mask complete, ivory-white, weakly shiny, lateral patches obliquely extended to the orbits beyond the antennal sockets. Foveae faciales distinct, reaching the vertex. Clypeus CL:CW 1.2, flat; surface silky shiny, shagreen with shallow, sparse punctation, anterior margin narrow, brown. Supraclypeal area white, protruding, apical part rhombic, apex set off from the frons. Frons and vertex with subcontiguous strong punctation, the narrow intervals glossy. Supraantennal area with small shiny surface. Genae striped with elongated punctation; occiput angular. Malae narrow. Labrum black, with flat callosity; the bifid mandibles black with brown tips.

**Mesosoma** normal, rounded; pilosity conspicuous, laterally and on the underside with erect white hairs. Coloration black, pronotum with two long yellow stripes, calli and tegulae with pale flecks. Pronotum not expanded, anterior margin medially narrow, dorsolateral angles sloping. Mesonotum and scutellum shagreen, matt, punctation moderate, dense; mesopleura densely setose, with punctation strong and close, anterior margin (omaulus) rounded. Legs black, with yellow anterior surface of foretibiae, tips of femora and tibial base and tip white, all basitarsi and second tarsomeres white; remaining tarsomeres blackened; wings brownish, venation black, costa dark. Propodeum evenly rounded; medial area rings demarcated by a row of meshes, surface with rough meshes; lateral areas finely wrinkled, matt; terminal area with finely sculptured surface, propodeal furrow narrow and deep.

**Metasoma** spindle-shaped, coloration black. T1 smooth and shiny, with punctation moderate, close; laterally with white fringe patches; T2 and following terga more finely and densely punctate; depressions paler. S3 with rounded-rectangular transverse callus, S4 transversely convex. Terminalia (Fig. 58): S7 with apical lobes proximally tapering with long bristles, laterally with a few bristles; S8 rhombiform, spiculum short, apex formed as a long extended narrow beak; genital capsule normal, gonoforcipes shorter than gonobase, apically blunt; penis valves of *brevicornis* type, in dorsal view shorter than the gonoforcipes.

**Female** (Fig. 54e–h). N = 1. TL 5.2 mm, WL 4.2 mm.

**Head**: Proportions HL:HW 0.89, outline heart-shaped, anterior face curved like a watch-glass. Pilosity less conspicuous than in the male. Scapes and pedicels black, flagella short, blackened above, yellow below. Mask ivory-white, with long-oval side stripes on the lower part of the orbits, below the scape bases. Foveae faciales long, reaching the vertex. Clypeus gently domed above, lower third strongly convex, apical margin bent up, with few long, protruding bristles; surface finely grained, matt, with shallow, coarse punctation; upper boundary indistinct. Supraclypeal area broad, rhombically expanded in the upper part, the lateral corners projecting, the tip tapering into the frons. Frons and vertex with subcontiguous strong punctation, intervals shiny; vertex with short setae. Genae normal, streaked with elongated punctation; occiput rounded; malae narrow. Labrum black, with flat annular cusp; mandibles trifid.

**Mesosoma** normal, rounded; pilosity comprises erect, short, white hairs laterally and on underside. Coloration black, pronotum with two yellow stripes, calli and tegulae with pale flecks. Pronotum not expanded, anterior margin medially narrow, dorsolateral angles sloping. Mesonotum and scutellum shagreen, silkily shiny, punctation anteriorly moderate subcontiguous, distally denser; mesopleura with punctation somewhat coarser and denser, omaulus rounded. Legs black, only tibiae bases yellow; wings brownish, venation black, costa brown. Propodeum evenly rounded; medial area reticulately-wrinkled, laterally demarcated by a row of meshes; lateral areas finely striate wrinkled, matt; terminal area with finely sculptured surface, propodeal furrow extended, open at the top.

**Metasoma** spindle-shaped, coloration black. T1 smooth and shiny, with punctation fine, scattered, apically somewhat denser, with lateral white fringe patches; T2 and following terga more finely and densely punctate. End fringe pale.

**Type material**: Holotype ♂, Nepal: Karnali, Gutichaur, 29°12'10"N 82°18'56"E, 2850 m, 09.06.1997, leg. F. Creutzburg. – Paratype ♀, ibid., Pahada, 29°04'33"N 82°41'42"E, 3010 m, 02–03.06.1997 both leg. F. Creutzburg, coll. SDEI.

**Etymology**: The species is named after the Nepalese village Gutichaur (Gothichaur) in the district of Jumla, where the specimens were collected.

### 22. *Hylaeus* (*Dentigera*) *kaigaonis* spec. nov.

urn:lsid:zoobank.org:act:9EFEF7EA-3BFE-4940-85D2-AA45D942DD00

**Diagnosis**: The male of the new species has strongly expanded, completely black scapes with a flat impression frontally; the mask is ivory-white. In females, the paraocular area has wedge-shaped spots.

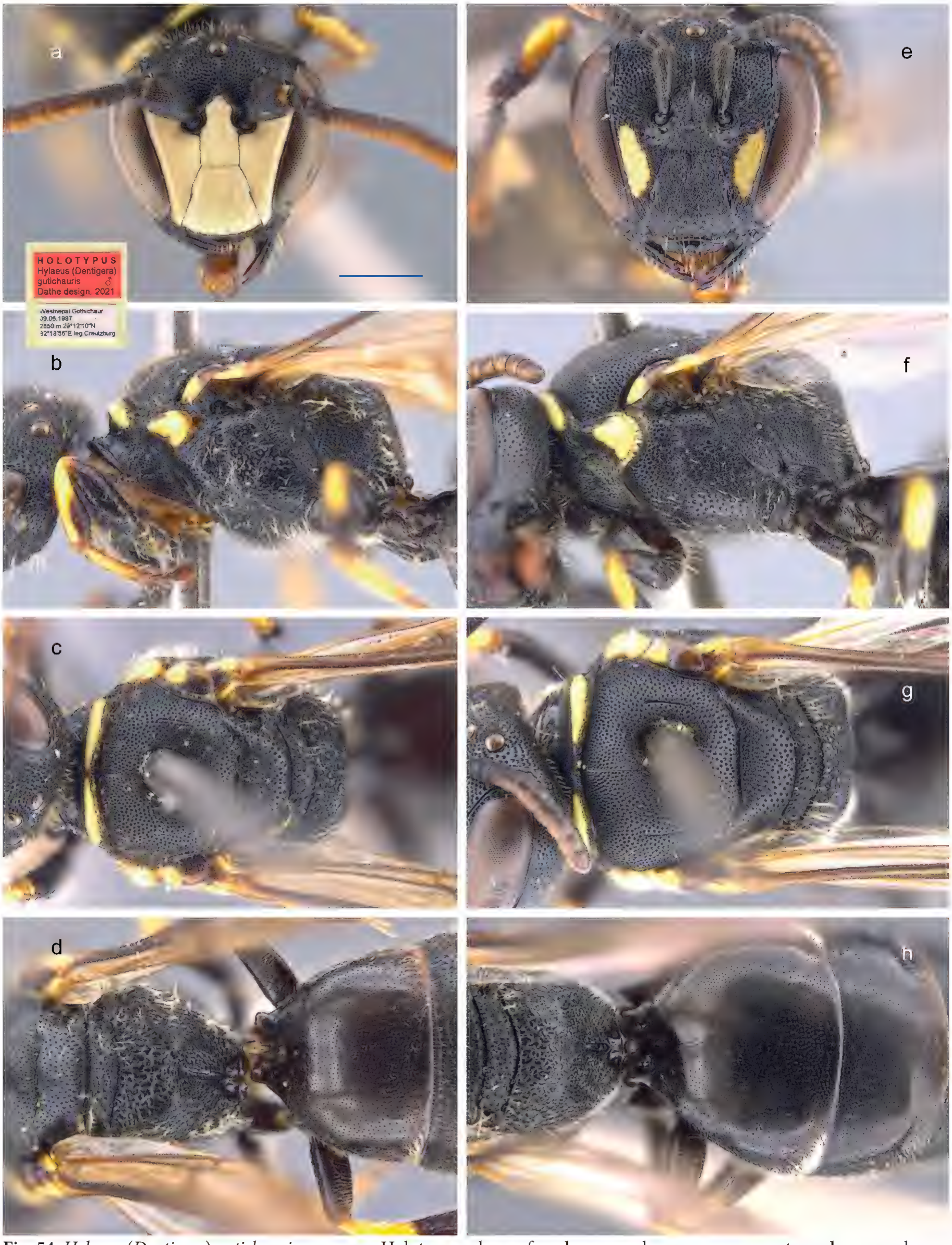



**Fig. 54**: *Hylaeus* (*Dentigera*) *gutichauris* **spec. nov.** Holotype male: **a** – face, **b** – mesopleuron, **c** – mesonotum, **d** – propodeums and metasoma base. Paratype female: **e** – face, **f** – mesopleuron, **g** – mesonotum, **h** – propodeums and metasoma base. – Scale bar: 0.5 mm.

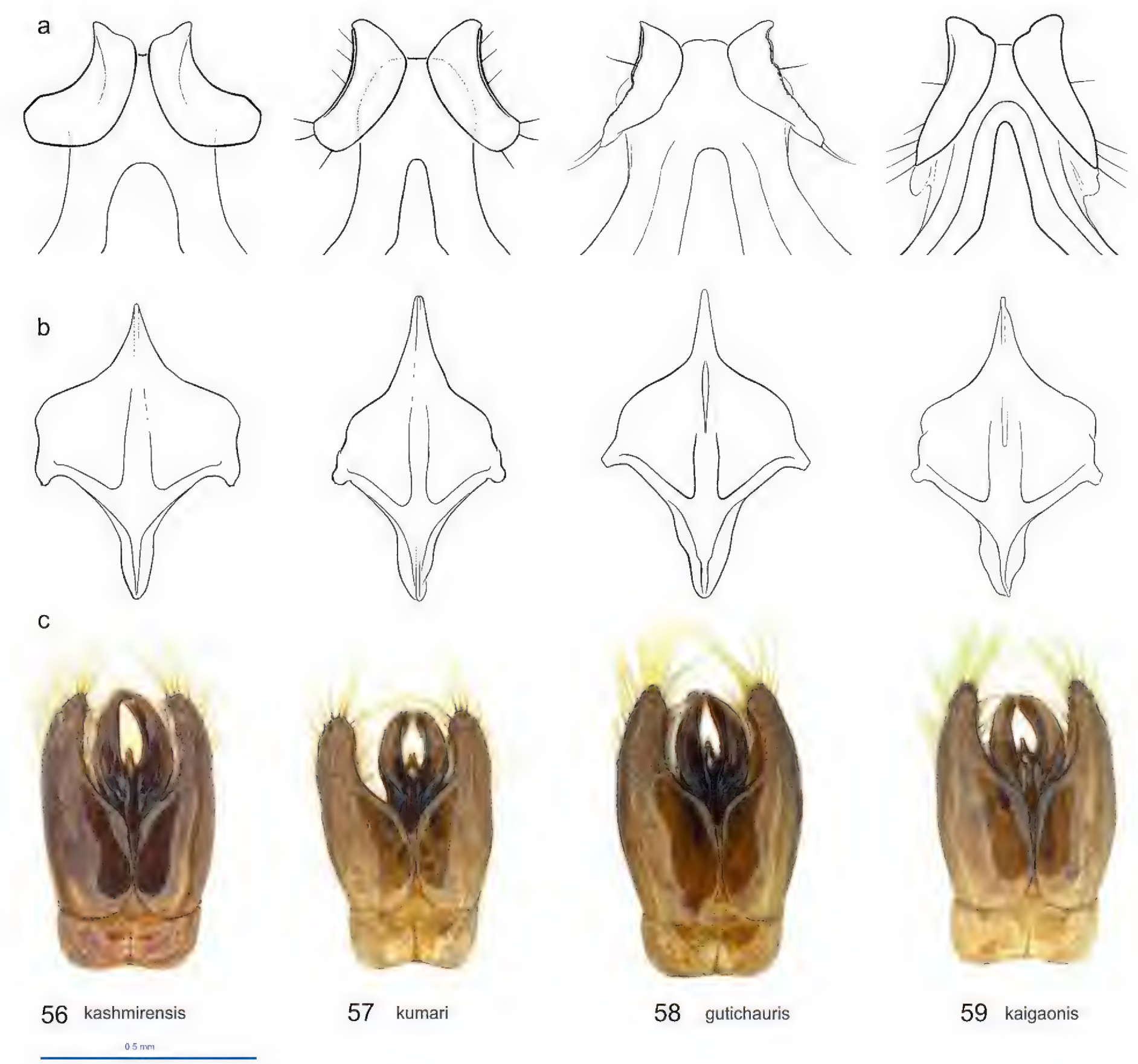
**Description: Male** (Fig. 55a–e). N = 1. TL 5.0 mm, WL 3.7 mm.

**Head**: Proportions HL:HW 0.92, UHW:LHW 1.50, outline trapezoid. Pilosity distinct, long and protruding. Scapes completely black without yellow dot at the tip, strongly expanded, ScL:ScW 1.6; backside flat, frontally in the middle with a flat impression, finely punctate, silky matt. Flagella short, black above, narrowly yellow below. Mask complete, ivory-white, weakly shiny, side patches bluntly expanded above, beyond the scape sockets. Foveae

**Fig. 55**: *Hylaeus* (*Dentigera*) *kaigaonis* **spec. nov.** Holotype male: **a** – face, **b** – mesopleuron, **c** – mesonotum, **d** – propodeum and metasoma base, **e** – metasoma ventral, S3 with hollowed callus. Paratype female: **f** – face, **g** – mesopleuron, **h** – mesonotum, **i** – propodeum and metasoma base. – Scale bar: 0.5 mm.

faciales distinct, reaching the vertex. Clypeus CL:CW 1.2, flat; surface silky shiny, shagreen with shallow, sparse punctation, anterior margin black. Supraclypeal area white, basally broad, apical part rhombic, apex set off from frons. Frons and vertex with subcontiguous strong punctation, the narrow intervals glossy. Supraantennal area with low glossy surface. Genae striate with elongated strong punctation; occiput edged. Malae narrow. Labrum black, with elliptic callosity; the bifid mandibles black with brown tips.

**Mesosoma** normal, rounded; pilosity conspicuous, laterally and on underside with erect, white hairs. Coloration black, pronotum with two yellow stripes, calli and tegulae with pale dots. Pronotum not expanded, anterior margin




**Figs 56–59**: Male terminalia of the Himalayan species of the *Hylaeus brevicornis* group. **56** – *kashmirensis*, **57** – *kumari*, **58** – *gutichauris* spec. nov., **59** – *kaigaonis* spec. nov. **a** – sternum 7, **b** – sternum 8, **c** – genital capsule. – S7 and S8 non-scale, genital capsules with scale bar: 0.5 mm.

medially narrow, dorsolateral angles sloping. Mesonotum and scutellum shagreen, matt, punctation strong, subcontiguous; mesopleura punctate like previous, dense vestiture of upstanding setae, anterior margin of mesopleura (omaulus) rounded. Legs black, with yellowish white anterior surface of foretibiae, tips of femora and tibial base white; basitarsi white, remaining tarsomeres blackened; wings brownish, venation black, costa brown. Propodeum evenly rounded, densely hairy laterally; medial area indistinctly demarcated by meshes, surface with rough meshes; lateral areas finely wrinkled, matt; terminal area with finely sculptured surface, propodeal furrow narrow and deep.

**Metasoma** spindle-shaped, coloration black. T1 smooth and shiny, only very fine shagreen, with punctation strong, close, denser towards the edge; laterally with white fringe patches; T2 and following terga more finely and densely punctate; depression pale. S3 with strong transverse, apically bipartite callus, S4 arched upwards. Terminalia (Fig. 59): S7 with apical lobes proximally prolongated, connected by lamella-like structures with the flanks, laterally with some short bristles; S8 rhombiform, spiculum wide, apex cuneiform; genital capsule normal, gonoforcipes clearly shorter than gonobase, apically converging; penis valves of *brevicornis* type, in dorsal view shorter than the gonoforcipes.

**Female** (Fig. 55f–i). N = 7. TL 5.4–5.9 mm, WL 3.7–4.0 mm.

**Head**: Proportions HL:HW 0.94, outline transverse-elliptical. Pilosity less conspicuous than in the male. Scapes and pedicels black, flagella short, blackened above, yellow below. Mask ivory-white, with wedge-

shaped side patches at the bottom of the orbits, extending upwards to the scape sockets. Foveae faciales long, reaching the vertex. Clypeus gently domed, margin upturned, with few long, protruding bristles; surface densely shagreen, dull, with shallow, strong punctation; upper demarcation indistinct. Supraclypeal area wide, rhombically expanded in the upper part, the corners projecting laterally, tapering into the frons. Frons and vertex with subcontiguous strong punctation, intervals smooth and shiny. Vertex with short setae. Genae normal, streaked with elongated moderate punctation; occiput rounded; malae narrow. Labrum black, with flat annular cusp; mandibles trifid.

**Mesosoma** normal, rounded; pilosity with erect short white hairs laterally and on underside. Coloration black, pronotum with two yellow stripes, calli and tegulae pale. Pronotum not expanded, anterior margin medially narrow, dorsolateral angles sloping. Mesonotum, scutellum and mesopleura shagreen, scarcely shiny, punctation moderately dense; omaulus rounded. Legs black, only with yellow tibia bases; wings brownish, venation black, costa dark. Propodeum evenly rounded; medial area basal with irregular longitudinal ridges, laterally hardly demarcated; lateral areas finely shagreen, matt; terminal area with finely sculptured surface, propodeal furrow narrow, open at the top.

**Metasoma** spindle-shaped, coloration black. T1 smooth and shiny, with fine, scattered punctation, apically somewhat denser, with white lateral fringe patches; T2 and following terga more finely and densely punctate. End fringe pale.

**Type material**: Holotype ♂, Nepal: Karnali, Kaigaun Umg., 29°06'43"N 82°35'32"E, 3000 m, 04.06.1997. – Paratypes 11 ♀♀, Nepal: Karnali, 2 ♀♀ Jumla Talphi, 29°20'03"N 82°22'34"E, 3115 m, 15.06.1997; 2 ♀♀ Maharigaon Umg., 29°21'30"N 82°23'46"E, 3725 m, 16.06.1997; 1 ♀ Maharigaon Umg., 29°20'24"N 82°23'21"E, 3345 m, 20.06.1997; 2 ♀♀ Jumla, Uthu, 2500 m, 22.06.1997; all leg. F. Creutzburg, coll. SDEI.

**Etymology**: The species is named after the Nepalese municipality Kaigaon (Kaigaun) in the district of Dolpa, where the specimens were collected.

## Annex

The following two species do not strictly belong to the *Hylaeus brevicornis* group, nor to any other: each stands alone. But they are added here for the sake of completeness, because *Hylaeus rubicola* SAUNDERS, 1850 was presented earlier as a member of the subgenus *Dentigera* in connection with the *Hylaeus conformis* group (DATHE 2006: 101–103).

### *Hylaeus* (*Dentigera*) *biarmicus* (WARNCKE, 1992)

*Prosopis* (*Nesoprosopis*) *biarmica* WARNCKE, 1992: 770, 799 ♂. Egypt: Sakkarah. Holotype OLM Linz.

*Hylaeus* (*Dentigera*) *biarmicus* (WARNCKE, 1992) – LHOMME et al. 2020: 66, 132.

**Diagnosis**: The author of the species knew only two males, one from Egypt (1897, coll. Schmiedeknecht) and one from Spain (Zamora). He compared these in detail with *Hylaeus pictipes* (by which he probably meant *Hylaeus taeniolatus*), then concluded that the species is closely related to *H. brevicornis*. At least he gave an illustration of the face, but this did not improve the recognizability of the species (compare Fig. 60a). However, the decisive character of this very small, gracile species is, in its entirety sharply margined terminal area of both sexes, in connection with a smooth, shiny integument of T1. The penis valves show an open cleft in dorsal view, but these parts are not curved but run parallel (Fig. 61c). The inner tooth is bluntly rounded and not visible from above, which does not correspond to the characters of the brevicornis group. However, the mandibles of the female are clearly tridentate, so that the classification into the subgenus *Dentigera* is at least not completely unjustified.

**Description of the female**

**Female new** (Fig. 60b–f). N = 1. TL 4.35 mm, WL 3.05 mm.

**Head**: Proportions HL:HW 0.89, UHW:LHW 1.48, outline heart-shaped. Pilosity short and sparse, erect. Scapes black, basally and laterally partly yellow; flagella blackened above, yellow below. Paraocular areas filled with triangular yellow spots reaching the level of the apex of the supraclypeal area, clypeus with small yellow spot; foveae faciales long, distinct. Clypeus CL:CW 1.08, finely shagreen, with coarse but shallow sparse punctation, anterior margin brown; supraclypeal area barely narrowed, gradually broadly merging into frons. Frons with strong dense punctation, including supra-antennal area, intervals of frons and vertex smooth, shiny. Genae longitudinally striped, shiny, with scattered punctation; occiput rounded; malae narrow. Labrum black, with small hump; mandibles trifid, blackish brown.

**Mesosoma** depressed; pilosity reduced, with short white hairs, erect on underside. Coloration black, pronotum with yellow band, calli totally, tegulae anteriorly yellow. Mesonotum and scutellum shagreen, matt, punctation strong, dense; mesopleura with punctation somewhat coarser and more scattered; omaulus rounded. Legs distally from the tip of the femur yellow including all tarsomeres; wings clear, venation light brown, stigma and subcosta dark. Terminal area of propodeum bordered all around with sharp-edged ledge (as in male); medial and lateral areas not delimited from each other, reticulately-wrinkled and shiny; propodeal medial furrow wide, sharply margined, smooth, upper part shagreen.

**Fig. 60**: *Hylaeus* (*Dentigera*) *biarmicus* (WARNCKE, 1992). **a** – male face; female new: **b** – face, **c** – propodeum, **d** – mesonotum, **e** – metasoma, **f** – mesopleuron. – Scale bar: 0.5 mm.

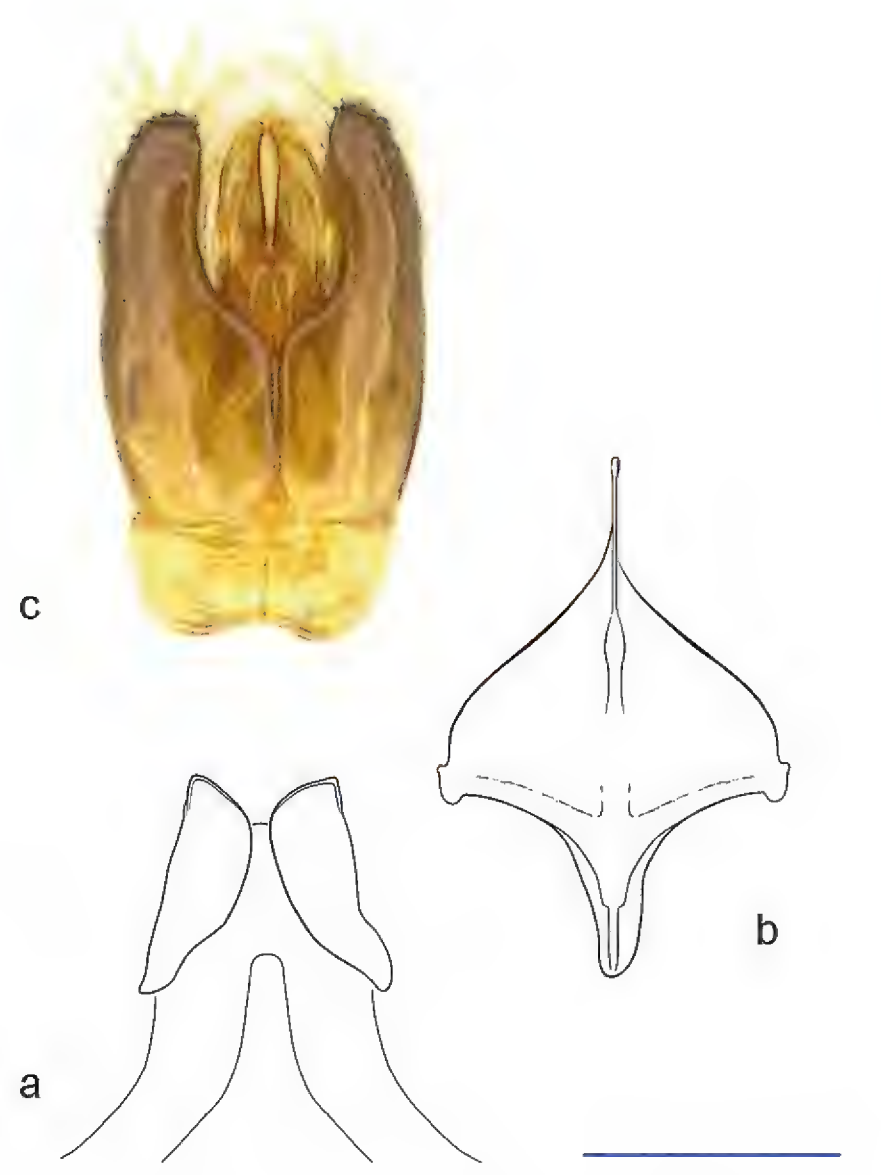



**Fig. 61**: Male terminalia of species not belonging to the *H. brevicornis* group: *Hylaeus* (*Dentigera*) *biarmicus* (WARNCKE, 1992). **a** – sternum 7, **b** – sternum 8, **c** – genital capsule. – S7 and S8 non-scale, genital capsules with scale bar: 0.5 mm.

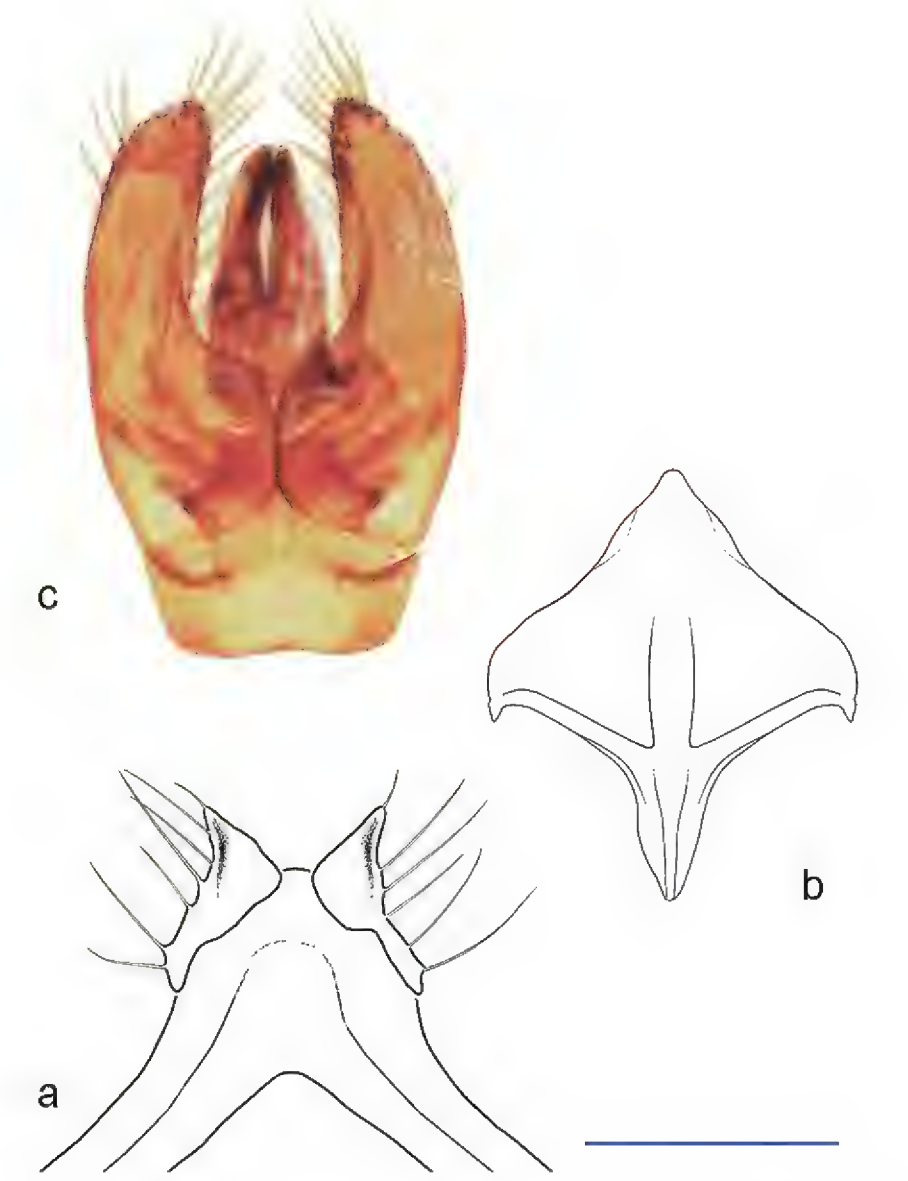



**Fig. 62**: Male terminalia of species not belonging to the *H. brevicornis* group: *Hylaeus* (*Dentigera*) *chukar* (WARNCKE, 1992), paratype. **a** – sternum 7, **b** – sternum 8, **c** – genital capsule. – S7 and S8 non-scale, genital capsules with scale bar: 0.5 mm.

**Metasoma** spindle-shaped, coloration black. T1 smooth and glossy, with moderate, close to sparse punctation; T2 and following terga finely shagreen, punctation finer and denser; terga laterally with white ciliar fringes, depressions transparent, horn brown. End fringe yellowish.

**Distribution**: Egypt: Sakkara. Spain: Zamora (Warncke 1992). New records: Spain: 1 ♂ Sierra de Maria, Almeria, 1400 m, 04.07.1994, F.J. Ortiz leg. Morocco: 1 ♂ Tizi-n-Test S, 1900 m, M. Schwarz leg.; 4 ♂♂ Bhalil, 10 km NW Sefrou, 28.05.1995, M. Halada leg.; 1 ♀ Fès-Meknès region, Beni Bassia, 60 km NE Boudnib, 21.05.1995, M. Halada leg., all coll. SDEI.

### *Hylaeus* (*Dentigera*) *chukar* (Warncke, 1992)

*Prosopis* (*Nesoprosopis*) *chukar* Warncke, 1992: 771–772 ♀♂. Turkey: Hakkâri, Serpil. Holotype ♀, OLM Linz.

*Hylaeus* (*Dentigera*) *chukar* (Warncke, 1992) – Özbek & Dathe 2020: 295, Fig. 2.

**Characters**: Small species with short, transversely oval head (female HL:HW 0.87). The most important diagnostic character of both sexes is the almost circularly expanded supraclypeal area, which merges flatly and broadly above into the frons. Setae on the clypeus are long, dense and upright. The propodeum is rounded, the basal area rimmed and has radially arranged fine longitudinal ribs, thus it merges into the terminal area in a rounded manner, as do the lateral areas. T1 very fine shagreen, shiny, with shallow fine sparse punctation. Male scape slender with pale apical spot; the mask white.

Male terminalia (Fig. 62); apical lobes of sternum 7 laced, at the outer edge with long fine bristles; sternum 8 short; the penis valves only slightly bent, the space between them narrow.

**Distribution**: Turkey: Hakkâri, 1800–3000 m.

## Discussion

The eponymous species of the *Hylaeus brevicornis* group is itself the biggest problem case in the group. To date, more than 30 synonyms have been assigned to the taxon. The current concept of the Nylander species was only recently stabilised by Erlandsson (1981), who designated a lectotype. One may well understand this "diversity" as a comfortable capitulation of the old authors in the face of the unusual difficulties posed by this species complex. The laudable exception is Förster (1871), who in turn went too far in his differentiation of taxa based on morphological details. Based on the rather small amount of material available to him, he could hardly evaluate intraspecific and interspecific variability, yet we nevertheless owe to him a relatively solid taxonomic basis.

Most later authors have hardly exerted themselves to get to the bottom of the problem. The proposal that *Hylaeus brevicornis* should be treated as a collective species goes back to Alfken (1905), who, with clear criticism of Förster's meticulousness, placed no less than 16 names as synonyms of *H. brevicornis* [with "*Prosopis atrata*" he meant *Hylaeus atratulus*]. Meade-Waldo (1923) adopted his complete list of synonyms, with the addition of further names. Warncke (1972), who did not know the latter paper, also adopted the complete Alfken list, but subdivided the nominal species into four subspecies with more or less geographical reference. However, he later retreated from this position as not "gerecht" [*just*, but meaning probably *justified*]: only a single species was involved, he concluded (Warncke 1981: 158). He extended the list of "known synonyms" to about 30 names, not infrequently by an "applicable description" (sic!). Finally, Warncke (1992) described "*Prosopis brevicornis*" as a polymorphic species, which at most varies geographically. He even defended this view vehemently towards dissenting opinions with personal insults, which cannot be tolerated in scientific articles.

Some previous authors were already much further ahead. Méhelÿ (1935) shows on his plate XIX clear differences in the terminalia of the *brevicornis* variants *imparilis*, *pallidicornis* and *kahri*. In the text (p. 152) *kahri* formally appears as a subspecies, but in the legends (p. 205) all four forms are handled as species, although he certainly did not mean to define their status in a strict taxonomic sense. Móczár (1960: 9.17 ♀, 9.29 ♂) in Fauna Hungariae also listed *imparilis*, *ambigua* and *kahri* as separate taxa, but as varieties of *brevicornis*. Finally, de Beaumont (1958: 166) expressed a quite decisive viewpoint; he recognised three forms in his Swiss material that "most probably represent three species", *Prosopis brevicornis* s. str., *P. kahri* and *P. gredleri*. The estate of Blüthgen (1880–1967), which he bequeathed to the Museum für Naturkunde Berlin, also contains sketches from around 1958 that could have put an end to the lumping. Unfortunately, none of them appeared in print. However, his findings were included in the cautious modern revision by Dathe (1980a).

The striking proof that *Hylaeus brevicornis* is a complex of species was provided by Schoder (2018). She found a unique situation on the site of Vienna's Nordbahnhof, which the designer of an experiment could not have arranged better to clearly disprove the notion of a single species: four (possibly even five) of the "synonyms" or "varieties" live syntopically side by side here, *Hylaeus brevicornis*, *H. gredleri*, *H. intermedius* and *H. imparilis* (possibly also *H. kahri*), and all of them could be reliably distinguished from each other genetically.

The syntopic occurrence of five very similar species naturally also gives rise to the thought that we see a polymorphic species. A comparable situation exists with certainty also at other places; so Wilhelm Grünwaldt

(in litt.) reported me already in the past sixties from his studies in Greece (Florina, Kalavryta). In fact, the intraspecific variation is comparatively large, so that overlaps can occur. This refers on the one hand to geographical variations, because quite a few species are widespread. They vary especially among the colonizers of islands, namely on the Aegean archipelago, where one can find just in some cases characteristic island forms. On the other hand, allometric relations play a role. In larger males, for example, the characteristic features such as expanded scapes, the ventral callosities on S3, and other sculpture characters are much more pronounced.

Among the approximately 50 Palaearctic *Hylaeus* species listed in the Barcode of Life Database (BOLD, Ratnasingham & Hebert 2007) are references to *H. brevicornis*, *H. glacialis*, *H. gredleri*, *H. imparilis*, *H. intermedius* and *H. kahri*. All these nominal taxa are well delimited clades. Together they form a monophylum *Dentigera*, which Schoder (2018) was able to further differentiate with her own investigations. According to this, (*H. brevicornis* + *H. imparilis*) appear as a pair facing *H. gredleri*. However, Schoder suspects ambiguity in *Hylaeus intermedius*, for which she found two clearly separated groups whose barcodes appeared next to those of *H. gredleri* on the one hand, and next to *H. kahri* on the other. For the latter, she assumes another cryptic species. In my morphologically based opinion, her "*intermedius* 2" corresponds to the true *H. kahri*, which was not included in her program. After all, it would be the fifth species at that locality and thus the full spectrum – actually a sensation. All taxa considered proved to be well defined, which was confirmed in connected morphometric examinations.

Our approach has been fully confirmed in these studies (Schmidt et al. 2015, Schoder 2018). Contrary to what Warncke (1992: 754) claimed, who assumed that intraspecific variability is the decisive factor "die typisch ist für die primitiven *Prosopis*-Arten", they are probably recently evolved forms that are still diversifying and spreading. This is indicated by their omnipresence in the western Palaearctic, their ecological adaptability and their high abundance in many places. Species development is obviously still in full swing, while morphological differences have not yet become pronounced. We can look forward to the results of the next phases of comprehensive gene sequencing.

## Acknowledgments

I would especially like to thank those who, over many years, have repeatedly entrusted me with their collections for identification and thus laid the foundation for my knowledge of the Palaearctic fauna. I would like to single out Werner Arens (Bad Hersfeld, D), Andreas W. Ebmer (Puchenau, A), Shuichi Ikudome (Kagoshima, JP), Timo Kopf (Bregenz, A), Yael Mandelik (Rehovot, IL), Hikmet Özbek (Bursa, TR), Theodora Petanidou (Mytilene, GR), Maxim Proshchalykin (Vladivostok, RU), Christian Schmid-Egger (Berlin, D), Maximilian Schwarz (Ansfelden, A), Bernard Vaissière (Avignon, F), including their teams.

The curators of major museums have generously supported me at all times, especially Julia Astafurova (ZISP St. Petersburg), Erich Diller (ZSS Munich), David Notton (NHM London), Michael Ohl (ZM Berlin), Martin Schwarz (OLM Linz), Claire Villemant (MNHN Paris) and Herbert Zettel (NHM Vienna). I am particularly grateful to the latter for his helpful advice in completing the manuscript.

Sincere thanks for active participation in this work also go to Stephan Blank (SDEI), who already in 1996 presented me all Förster types, to Frank Creutzburg (Jena), Michael Kuhlmann (Kiel), Andreas Müller (Zurich), Christophe Praz (Neuchatel) and last but not least Sabine Schoder (Vienna).

Andrew Liston (SDEI) is thanked for his language check of this manuscript and factual advice. The Senckenberg Gesellschaft für Naturfoschung (SGN), Frankfurt am Main, again generously supported my work.

## References

Alfken, J. D. 1905: Die Förstersche Monographie der Bienen-Gattung *Hylaeus* F. (Latr.) = *Prosopis* F. und die *Prosopis*-Sammlung Försters. – Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen **18** (1904): 108–124.

Alfken, J. D. 1936a: Neue *Prosopis*-Arten vom Libanon. – Konowia **15**: 51–53.

Alfken, J. D. 1936b: Beitrag zur Kenntnis der *Prosopis*-Arten von Tadzhikistan und Turkmenien. – Veröffentlichungen aus dem Deutschen Kolonial- und Uebersee-Museum Bremen **1** (3): 384–388.

Alfken, J. D. 1938: Ein weiterer Beitrag zur Kenntnis der Bienenfauna von Palästina mit Einschluß des Sinai-Gebirges (Hym. Apid.). – Deutsche Entomologische Zeitschrift 1938 (2): 418–433.

Aliev, H. A. 1986: A synopsis of the bee genus *Hylaeus* Fabricius 1793 of Soviet Azerbaidjan (Insecta: Hymenoptera: Apoidea: Colletidae). – Senckenbergiana biologica **66** (4/6): 261–269.

Beaumont, J. de 1958: Les Hyménoptères aculéates du Parc National Suisse et des régions limitrophes. – Ergebnisse der wissenschaftlichen Untersuchungen des Schweizerischen Nationalparks **VI** (Neue Folge): 145–235.

Benoist, R. 1959: Les *Prosopis* de France (Hyménoptères Apidés). – Cahiers des Naturalistes, Paris N.S. **15** (3): 75–87.

Bertsch, A. 2019: The subgenera of European bumblebees (*Bombus*) and the genital capsule of males. – EBook. – ISBN 978-3-947278-02-2, 978-3-947278-03-9. – https://www.bombus4you.de/ebook/english.htm.

Bertsch, A. & Titze, A. 2019: The genital capsule of selected European bumblebee males (*Bombus*) A collection of 600 SEM images (Scanning Electron Microscope). – Florian Bertsch, Leipzig. 316 pp., 630 SEM figs. – ISBN 978-3-947278-40-4.

BOLD 2011: Barcode of Life Data System v. 4, www.boldsystems.org. TaxonID (*Colletes*; *Hylaeus*), accessed 02 November 2011.

Boustani, M.; Rasmont, P.; Dathe, H. H.; Ghisbain, G.; Kasparek, M.; Michez, D.; Pauly, A.; Risch, S.; Straka, J.; Terzo, M.; van Achter, X.; Wood, T. J. & Nemer, N. 2021: The bees of Lebanon (Hymenoptera: Apoidea: Anthophila). – Zootaxa **4976** (1): 1–146. – doi.org/10.11646/zootaxa.4976.1.1.

Chen, X. & Xu, H. 2009: A key to species of the genus *Hylaeus* (Hymenoptera: Colletidae) from mainland of China with descriptions of new species and new records. – Zootoxa **1974**: 31–50.

Constantinescu, A. 1973: Contributions à l'étude de l'armature génitale du mâle chez les espèces de *Prosopis* F. (Hym. Apoidea). I. – Travaux du Muséum d'Histoire Naturelle «Grigore Antipa» **13**: 254–263. – (1974): Part II. Ibid. **14**: 195–207.

Dalla Torre, C. G. de 1896: Catalogus Hymenopterorum hucusque descriptorum systematicus et synonymicus. Vol. X. Apidae (Anthophila). – Engelmann, Lipsiae. VIII + 643 pp. [*Prosopis* p. 13-35].

Dathe, H. H. 1980a: Die Arten der Gattung *Hylaeus* F. in Europa (Hymenoptera: Apoidea, Colletidae). – Mitteilungen aus dem Zoologischen Museum Berlin **56**: 207–294.

Dathe, H. H. 1980b: Die *Hylaeus*-Arten einer apidologischen Sammelreise in den Iran (Hymenoptera, Apoidea). – Entomologische Abhandlungen, Dresden **43**: 77–97.

Dathe, H. H. 1986: Die Bienengattung *Hylaeus* Fabricius in der Mongolei (Hymenoptera: Apoidea, Colletidae). – Annales historico-naturales Musei nationalis Hungarici **78**: 265–300.

Dathe, H. H. 2006: Studien zur Systematik und Taxonomie der Gattung *Hylaeus* F. (5). Revision der Hylaeus-conformis-Gruppe (Apidae, Colletinae). – Beiträge zur Entomologie, Keltern **56** (1): 63–91.

Dathe, H. H. 2009: Anmerkungen zu Bau und Funktion sexualdimorpher Antennenstrukturen in der Gattung *Hylaeus* F. (Hymenoptera, Anthophila, Colletidae). – Entomologische Nachrichten und Berichte **53** (3/4): 151–156.

Dathe, H. H. 2010: Studien zur Systematik und Taxonomie der Gattung *Hylaeus* F. (6). Arten asiatischer Hochgebirge und Anmerkungen zu weiteren asiatischen Arten (Hymenoptera, Anthophila, Colletidae). – Linzer biologische Beiträge **42** (1): 43–80.

Dathe, H. H. 2015: Studies on the systematics and taxonomy of the genus *Hylaeus* F. (10). New descriptions and records of Asian *Hylaeus* species (Hymenoptera: Anthophila, Colletidae). – Contributions to Entomology **65** (2): 223–238.

Dathe, H. H.; Kuhlmann, M. & Villemant, C. (eds.) (2012): Hippolyte Janvier, Comportements d'Abeilles Colletidae (Hymenoptera). Les genres *Hylaeus, Chilicola, Colletes, Pasiphae, Policana, Cadeguala, Caupolicana, Lonchopria* et *Diphaglossa*. Historical reprint of the manuscript of the Muséum National d'Histoire Naturelle, Paris, with annotations by Holger H. Dathe; Michael Kuhlmann & Claire Villemant. – Entomofauna, Monographie **2**: I-VII, 1–181. – ISSN 0250-4413.

Dathe, H. H. & Proshchalykin, M. Yu. 2016: The genus *Hylaeus* Fabricius in Mongolia, an updated species inventory (Hymenoptera: Apoidea, Colletidae). – Zootaxa **4121** (4): 351–382.

Dathe, H. H. & Proshchalykin, M. Yu. 2017: Type revision of Asiatic bees of the genus *Hylaeus* F. described by Ferdinand Morawitz (Hymenoptera: Apoidea, Colletidae). – Zootaxa **4227** (1): 1–48. – doi.org/10.11646/zootaxa.4227.1.1.

Dathe, H. H. & Proshchalykin, M. Yu. 2018: The genus *Hylaeus* Fabricius in Central Asia (Hymenoptera: Apoidea: Colletidae). – Zootaxa **4517** (1): 1–91. – dx.doi.org/10.11646/zootaxa.4517.1.

Erbe, G. 2011: Beobachtungen bei Maskenbienen eines Hausgartens im südöstlichen Mittelfranken. – https://www.guntramerbe.de/maskenbienen/index.html.

– video 16 2011 08 12 hylaeus spec allium montanum antennenkontakt 1. – https://www.youtube.com/watch?v=Q1qTuL3MCz8.

– video 17 2012 08 05 hylaeus spec allium montanum antennenkontakt 2, https://www.youtube.com/watch?v=n-4CAxMLJvY-.

Erlandsson, S. 1981: Designation of the lectotypes of *Hylaeus brevicornis* Nylander, 1852 and *Hylaeus pictipes* Nylander, 1852 (Hymenoptera, Apidae). – Notulae Entomologicae **61**: 177–178.

Förster, A. 1871: Monographie der Gattung *Hylaeus* F. (Latr.). – Verhandlungen der k. k. Zoologisch-Botanischen Gesellschaft in Wien **21**: 873–1084.

Ikudome, S. & Dathe, H. H. 2021: Two new species and some new records of the genus *Hylaeus* (Hymenoptera: Apoidea, Colletidae). – Bulletin of the Institute of Minami-kyushu Regional Science **37**: 1–10.

Lázaro, A.; Praz, C.; Müller, A.; Ebmer, A. W.; Dathe, H. H.; Scheuchl, E.; Schwarz, M.; Risch, S.; Pauly, A.; Devalez, J.; Tscheulin, T.; Gómez-Martínez, C.; Papas, E. & Petanidou, T. 2021: Impacts of beekeeping on wild bee diversity and pollination interactions in the Aegean Archipelago. – Ecography **44** (5): 1–13. – doi.org/10.1111/ecog.05553; – dx.doi.org/10.5061/dryad.ns1rn8psn.

Leclercq, J. 1964: Données pour un atlas des Hyménoptères de l'Europe occidentale. – Bulletin de l'Institut Agronomique et des Stations de Recherches de Gembloux **32** (1): 36–70.

Lhomme, P.; Michez, D.; Christmann, S.; Scheuchl, E.; El Abdouni, I.; Hamroud, L.; Ihsane, O.; Sentil, A.; Chrif Smaili, M.; Schwarz, M.; Dathe, H. H.;

Straka, J.; Pauly, A.; Schmid-Egger, C.; Patiny, S.; Müller, A.; Praz, C.: Risch, S.; Kasparek, M.; Kuhlmann, M.; Wood, T. J.; Bogusch, P.; Ascher, J. & Rasmont, P. 2020: The wild bees (Hymenoptera: Apoidea) of Morocco. – Zootaxa **4892** (1): 1–159. – doi.org/10.11646/zootaxa.4892.1.1.

Meade-Waldo, G. 1923: Hymenoptera, Fam. Apidae, Subfam. Prosopidinae. – In: Wytsman, P. (Ed.), Genera Insectorum. Vol. **181**. – Tervueren, Brussels: 45 pp.

Méhelÿ, L. 1935: Naturgeschichte der Urbienen. – Stephaneum, Budapest: 214 pp., 60 pls.

Michener, C. D. 2007: The bees of the world. 2nd Edition. Johns Hopkins University Press, Baltimore: xvi + [i] + 953 pp., 20 pls.

Móczár, M. 1960: Ösméhek – Földi Méhek. Colletidae – Melittidae. – Fauna Hungariae. Vol. XIII, Hymenoptera III (9): 9.1–9.64 [in Hungarian].

Morawitz, F. 1872: Ein Beitrag zur Bienenfauna Deutschlands. – Verhandlungen der k. k. Zoologisch-Botanischen Gesellschaft in Wien **22**: 355–388.

Morawitz, F. 1876: Bees (Mellifera). – In: A travel to Turkestan by the member-founder of the society A.P. Fedtschenko accomplished from the Imperial society of naturalists, anthropologists, and ethnographists on a commission from the general-governor of Turkestan K. P. von Kaufmann. Issue 13. Vol. II. Zoogeographical Investigations. Pt. V. (Division 7). – M. Stanyukevich's Printing house, Moscow, pp. 161–303, 3 pls. [Proceedings of the Royal Society of Amateurs of Natural History Sciences, Anthropology and Ethnography **21** (3) [in Russian].

Nilsson, L. A. 2007: The type material od Swedish bees (Hymenoptera, Apoidea) I. – Entomologisk Tidskrift **128** (4): 167–181.

Nurse, C. G. 1903: New species of Indian aculeate Hymenoptera. – The Annals and Magazine of Natural History **11** (7): 393–403, 511–526, 528–549.

Nylander, W. 1852: Revisio synoptica Apum borealium, comparatis speciebus Europae mediae. – Notiser ur Sällskapets pro Fauna et Flora Fennica Förhandlingar **2**: 225–286.

Osytchnjuk, A. Z. 1970: Fauna Ukraini. Tom **12**. Bdzolini vyp. 4. Bdzoli-koletidi. – Naukova Dumka, Kiev: 158 pp. [in Ukrainian].

Osytchnjuk, A. Z.; Panfilov, D. V. & Ponomareva, A. A. 1978: Superfamily Apoidea. – In: Medvedev, G. S. (Ed.), Key to the Insects of the European Part of the USSR. Vol. **III**. Hymenoptera. Pt. 1. – Nauka, Leningrad, pp. 279–519. [in Russian].

Özbek, H. & Dathe, H. H. 2020: The bees of the genus *Hylaeus* Fabricius, 1793 of Turkey, with keys to the subgenera and species (Hymenoptera: Anthophila, Colletidae). – Contributions to Entomology, Keltern **70** (2): 273–346.

Pérez, J. 1903: Espèces nouvelles de Melliféres. – Procés-verbaux de la Société Linnéenne de Bordeaux **58**: 78–93, 208–236.

Popov, V. B. 1939: Subgeneric groupings of the genus *Prosopis* F. (Hymenoptera). – Comptes Rendus (Doklady) de l'Academie des Sciences de l'URSS **25** (2): 167–170.

Popov, V. B. 1949: Notes on the bee fauna of Tajikistan (Hymenoptera, Apoidea). – Trudy Zoologicheskogo Instituta Leningrad Akademii Nauk SSSR **8**: 688–699. [in Russian].

Proshchalykin, M. Yu. 2017: Family Colletidae. – In: Lelej, A. S.; Proshchalykin, M. Yu. & Loktionov, V. M. (eds.), Annotated catalog of the Hymenoptera of Russia. Vol. **I**. Symphyta and Aculeata. – Russkaya kollektsiya SpB, St. Petersburg, pp. 257– 262. [Proceedings of the Zoological Institute RAS, Supplement 6].

Proshchalykin, M. Yu. & Dathe, H. H. 2012: The bees of the genus *Hylaeus* Fabricius 1793 of the Asian part of Russia, with a key to species. – Zootaxa **3401**: 1–36.

Proshchalykin, M. Yu. & Dathe, H. H. 2016: Additional records of the genus *Hylaeus* Fabricius, 1793 (Hymenoptera: Apoidea: Colletidae) from Siberia, with description of a new species. – Zootaxa, **4105** (4): 301–320. – doi.org/10.11646/zootaxa.4105.4.1.

Proshchalykin, M. Yu. & Dathe, H. H. 2017: New records of bees of the genus *Hylaeus* Fabricius (Hymenoptera: Colletidae) in the European part of Russia and North Caucasus. – Proceedings of the Russian Entomological Society, St. Petersburg **88** (2): 61–65.

Proshchalykin, M. Yu. & Dathe, H. H. 2018: In the footsteps of history: the bees of the genus *Hylaeus* Fabricius (Hymenoptera, Apoidea: Colletidae) collected by V. I. Roborovsky and P. K. Kozlov in Northwest China (1895–1926). – Zootaxa **4434** (3): 573–588.

Proshchalykin, M. Yu. & Dathe, H. H. 2021: New and little-known bees of the genus *Hylaeus* Fabricius, 1793 (Hymenoptera: Colletidae) from the Caucasus region. – Journal of Hymenoptera Research **84**: 169–185. – doi.org/10.3897/jhr.84.68250.

Rasmont, P.; Ebmer, A. W.; Banaszak, J. & van der Zanden, G. 1995: Hymenoptera Apoidea Gallica. Liste taxonomique des abeilles de France, de Belgique, de Suisse et du Grand-Duché de Luxembourg. – Bulletin de la Societé entomologique de France **100** (hors série): 1–98.

Ratnasingham, S. & Hebert, P. D. N. 2007: BOLD. The Barcode of Life Database (www.barcodinglife.org). – Molecular Ecology Notes **7**: 355–364.

Saunders, S. S. 1850: Descriptions of two new Strepsipterous insects from Albania parasitical on bees of the genus *Hylaeus*; with some account of their habits and metamorphosis. – Transactions of the Royal Entomological Society of London **2** (1): 43–59.

SCHMIDT, S.; SCHMID-EGGER, C.; MORINIÈRE, J.; HASZPRUNAR, G. & HEBERT, P. D. N. 2015: DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees. – Molecular Ecology Resources **15** (4). – Wiley Online Library. – doi.org/10.1111/1755-0998.12363.

SCHODER, S. 2018: The *Hylaeus brevicornis* group revisited – an integrative approach to delimit four closely related species of masked bees (Hymenoptera: Apidae). – Master's Thesis. Universität Wien: 43 pp.

SCHULZ, W. A. 1906: Die Hymenopteren der Insel Creta. – Spolia Hymenopterologica: pp. 48–75. Paderborn, A. Pape.

SCHWARZ, M.; GUSENLEITNER, F.; WESTRICH, P. & DATHE, H. H. 1996: Katalog der Bienen Österreichs, Deutschlands und der Schweiz (Hymenoptera, Apidae). – Entomofauna, Linz/München, Suppl. **8**: 398 pp.

SMITH, F. 1876: Catalogue of British Hymenoptera in the collection of the British Museum. Andrenidae and Apidae. 2nd ed., part 1, XI + 236 pp., 11 pls. – London.

TORCHIO, P. F. 1984: The nesting biology of *Hylaeus bisinuatus* FÖRSTER and development of its immature forms (Hymenoptera: Colletidae). – Journal of the Kansas Entomological Society **57** (2): 276–297.

WARNCKE, K. 1972: Beitrag zur Systematik und Verbreitung der Bienengattung *Prosopis* F. in der Westpaläarktis (Hymenoptera, Apoidea, Colletidae). – Bulletin des Recherches agronomique de Gembloux, New Series **5**: 746–768 [1970].

WARNCKE, K. 1981: Beitrag zur Bienenfauna des Iran 12. Die Gattung *Prosopis* F., mit Bemerkungen zu weiteren bekannten und unbekannten paläarktischen Arten. – Bollettino del Museo Civico di Storia Naturale di Venezia **31**: 145–195 [1980].

WARNCKE, K. 1992: 2. Beitrag zur Systematik und Verbreitung der Gattung *Prosopis* F. in der Westpaläarktis (Hym., Apidae). – Linzer biologische Beiträge **24** (2): 747–801.